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HYDRARCH SUCCESSION AND [illegible] PRODUCTION

OF [illegible] LAKES IN CENTRAL ALBERTA

by

© [illegible] GERARD VAN DER [illegible]

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF [illegible]

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

HYDRARCH SUCCESSION AND PRIMARY PRODUCTION OF OXBOW LAKES IN CENTRAL ALBERTA

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© ARNOLD GERARD VAN DER VALK

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SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

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SPRING, 1970

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FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled HYDRARCH SUCCESSION AND PRIMARY PRODUCTION OF OXBOW LAKES IN CENTRAL ALBERTA submitted by Arnold Gerard van der Valk in partial fulfilment of the requirements for the degree of Master of Science.

Abstract

The plant communities in a series of 15 oxbow lakes cut off by the Pembina River in central Alberta were examined to determine their successional sequence and productivity. These oxbows can be characterized as hard water lakes: pH 8.4-8.8, total alkalinity 90-170 ppm $CaCO_3$, total hardness 90-165 ppm $CaCO_3$, conductivity *ca.* 300 μmhos, and 20-30 ppm sulfate. Their sediments are predominantly clay loams or clays, plus some silty and sandy clay loams with a basic pH (7.4-7.8) which reflects the limestone parent material from which they originated, as does their base exchange capacity (Ca^{++}, Mg^{++}, Na^{+}, and K^{+} vary from 8-22, 4-10, 0.4, and 0.5-2.0 meq/100 g of sediment respectively).

Water chemistry and water level fluctuations caused by periodic flooding are the major factors controlling plant distribution and succession.

Eleven communities were recognized as a result of cluster and factor analyses carried out on the phytosociological data: three submerged (*Potamogeton pectinatus*, mixed submerged, and *Potamogeton pectinatus-Ceratophyllum demersum*); two floating leaved (*Potamogeton natans* and *Nuphar variegatum*); four emergent (*Equisetum fluviatale*, *Eleocharis palustris*, *Alisma plantago-aquatica*, and *Typha latifolia*); and three meadow (*Carex-Acorus calamus*, *Carex-Bryoid*, and *Acorus calamus-Sonchus uliginosus*).

The successional sequence in these oxbows follows one basic pattern: *Potamogeton pectinatus*, *P. zosteriformis*, *P. richardsonii*, and *Ceratophyllum demersum*→*Potamogeton*

pectinatus→*Nuphar variegatum* or *Potamogeton natans*→*Equisetum fluviatale*, *Typha latifolia* or *Alisma plantago-aquatica* and *Eleocharis palustris*→*Carex* meadows→*Salix* shrub→*Salix* forest→*Populus balsamifera*.

The maximum above ground standing crop of communities follows a definite pattern with succession: from submerged (*ca*. 200 g/m^2), through floating leaved (*ca*. 210 g/m^2), to the emergent community (*ca*. 465 g/m^2) there is a stepwise increase in annual production, which declines in the meadow community (*ca*. 325 g/m^2).

Leaf area index does not change with succession: it remains between 3 and 4 in all the stages examined. Chlorophyll follows a pattern similar to standing crop, except that submerged communities contain more chlorophyll than floating leaved: submerged (240-916 mg/m^2), floating leaved (293-797 mg/m^2), emergents (622-2,127 mg/m^2), and meadow (542-1,414 mg/m^2).

The differences in standing crop, and by extension productivity, of these communites with succession appears to be the result of a combination of factors: differences in light intensity, rates of CO_2 diffusion, nutrient availability are responsible for the major differences between aquatic and semi-aquatic communities. Productivity is also a function of the height and structure of the plant community.

Acknowledgements

I would like to thank my supervisor, Dr. L. C. Bliss, for his advice and encouragement during the field and final stages of this study.

Miss Madeleine Dumais confirmed and corrected the identifications of the vascular species; Drs. Paul and Muriel Stringer identified the bryophytes; the Alberta Institute of Pedology, the Alberta Soil Survey, and the Department of Soil Science, University of Alberta provided facilities for soil analyses and the use of two unpublished soil maps. To these people and organizations, as well as the people of the Pembina River valley, I express my sincere thanks.

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Introduction

Lindeman (1942) in his classic paper on "The trophic dynamic aspect of ecology" tentatively outlined the changes that occur during succession in the annual production of communities. He suggested that there is an increase in annual production until a lake becomes senescent. With senescence there occurs a marked decline in annual production, but subsequent terrestial communities increase in annual production with a levelling off or slight reduction at climax. Evidence collected by Penfound (1956), and especially Westlake (1963, 1965), suggests that such a pattern does exist in succession. Westlake postulates that there is a steady rise in annual production in aquatic and semi-aquatic stages, up to and including the emergent community, at which point the annual production drops significantly.

The data which Westlake (1963, 1965) presents to illustrate this pattern have, by necessity, been taken from studies done at a variety of sites. The only study which includes aquatic, emergent, and meadow communities published to date, Bray (1960), fails to show the pattern. The present study was undertaken to test Westlake's hypothesis.

A series of oxbow lakes was selected for this investigation, since oxbows, because of their identical origin, have a similar basin morphometry; and since located in the same area, they should be subject to very similar environmental conditions. Besides a uniformity of conditions, oxbow lakes offer several other distinct advantages for this type of successional study. They are generally very shallow lakes in

which aquatic macrophytes are the dominant vegetation due to the virtual elimination of algae through competition (Westlake 1963). This greatly simplifies sampling since algae can be ignored without introducing a significant error. Oxbows allow a replication of samples from a number of lakes insuring a more representative sampling. It is also possible to determine the actual sequence of succession by examining oxbows of different ages, rather than presuming that zonation reflects succession.

Three basic types of data were gathered in the oxbows: floristic data to allow comparisons between communities and to establish the successional sequence; physical and chemical data to insure that these oxbows were similar in more than just basin morphometry, and to follow changes in the oxbows that occur as a result of succession; and productivity data in the form of standing crop harvests, three times during the growing season, plus chlorophyll and leaf area index measurements. Chlorophyll and leaf area measurements were taken to assess their role in determining the changes which occur in annual production with succession, since both of these parameters appear to play a prominent role in controlling community production (Aruga and Monsi 1963).

Nomenclature in this study follows Moss (1959) for all vascular species and Bird (1963, 1968) for all bryophytes. Voucher specimens are deposited in the University of Alberta Herbarium.

Description of Study Area

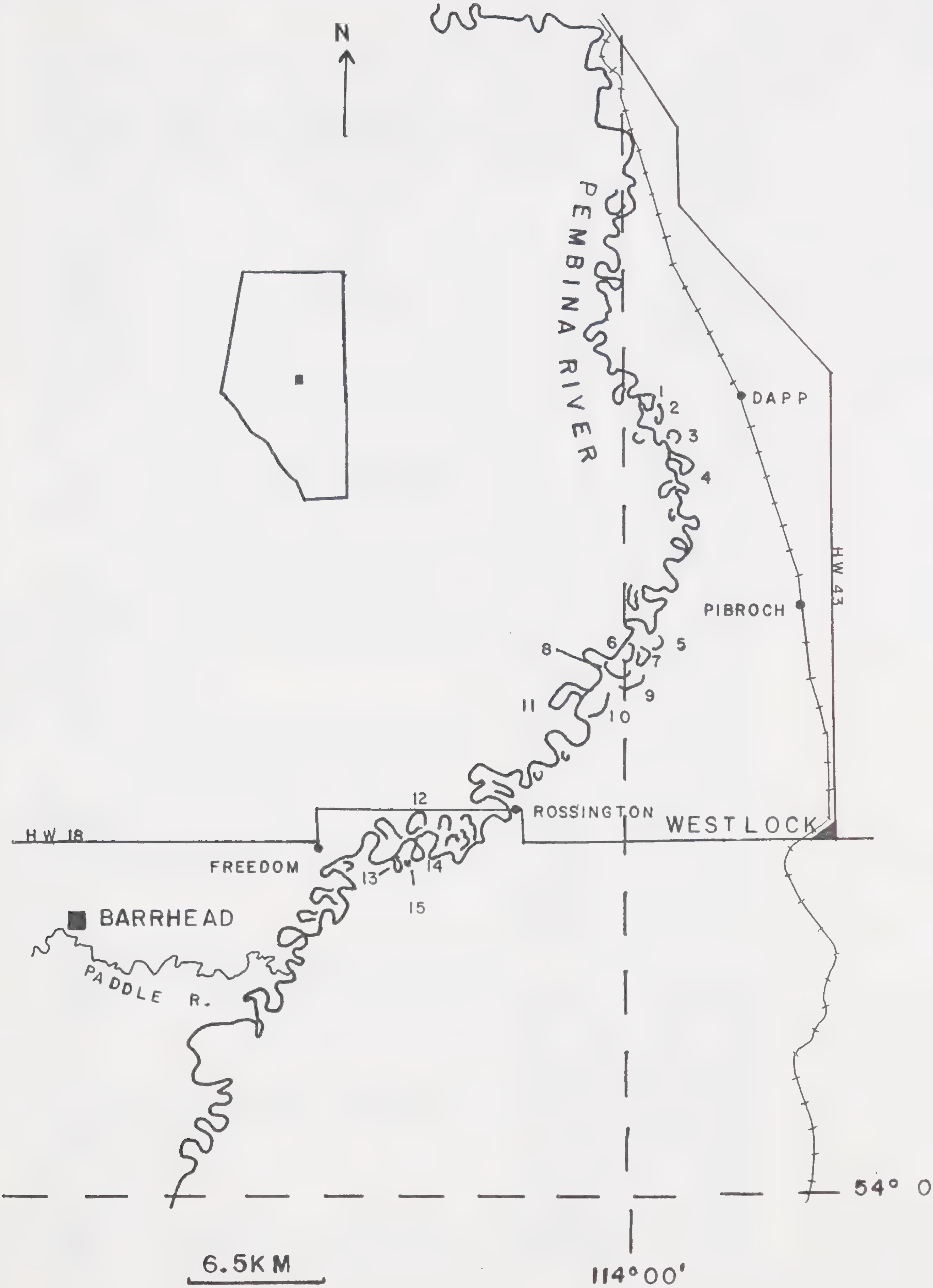
I. Selection and Location of Study Area

In the summer of 1968, using aerial photographs and maps, a series of rivers was located along which there were concentrations of oxbow lakes. This was followed by a surface reconnaissance to determine feasilibity. All areas except the Pembina River valley in central Alberta between Barrhead and Jarvie were eliminated for logistic reasons. The Pembina River valley was chosen because of: (1) a large concentration of oxbows within a relatively short distance (more than 30 oxbows in less than 30 km); (2) a number of recently created artificial oxbows, resulting from a river straightening scheme of the Alberta Water Resources Division; and (3) ready accessibility to the area (only 75 km from Edmonton). The only drawback of this area, over most of the others considered, is disturbance by man. Most of the area is under cultivation or used for grazing livestock.

The geographic location of the study area is shown in Fig. 1. In terms of the Alberta Land Survey, this area is in townships 59 through 63 and ranges 27 east and 1 and 2 west of the fifth meridian, or between parallels of latitude 54° 8' and 54° 25' and longitude 113° 55' and 114° 12'.

The Pembina River has its origins in the foothills region of the Cordillera east of Jasper. It flows approximately north-west, and later north, until it joins the Athabasca River north-west of Flatbush. In its upper course, the Pembina has a rather steep gradient, but in its middle and lower courses, a rather shallow gradient. The oxbow

Figure 1. Map of the study area.



N
PEMBINA RIVER
DAPP
PIBROCH
HW 43
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
ROSSINGTON
WESTLOCK
HW 18
FREEDOM
BARRHEAD
PADDLE R.
54° 0
6.5KM
114°00'

Table 1. Lake basin morphometry and watershed land use for the fifteen intensively studied oxbow lakes.

OXBOW NUMBER	ORIGIN OF[1] BASIN	AVERAGE[2] DEPTH (m)	MAXIMUM DEPTH (m)	WATERSHED LAND USE[3] CULT.	GRAZING (%)	FOREST	SUSCEPTIBILITY[4] TO FLOODING	AGE OF[5] LAKE
1	A	1.0	2.0	50	30	20	1	3 yrs.
2	N	1.0	1.5	85	5	10	3	old
3	N	2.0	3.5	30	10	60	2	int.
4	A	1.0	1.0	50	--	50	1	11 yrs.
5	N	0.8	1.0	60	--	40	2	int.
6	N	1.8	2.5	30	--	70	2	int.
7	N	1.5	1.8	60	--	30	2	int.
8	N	1.2	1.8	90	--	10	2	int.
9	N	1.2	1.8	50	5	45	2	int.
10	N	0.5	1.0	50	--	50	3	old
11	A	0.5	1.0	80	--	20	1	10 yrs.
12	N	1.5	3.0	60	--	40	2	int.
13	A	0.5	2.8	70	--	30	1	4 yrs.
14	A	0.8	4.0	95	--	5	1	4 yrs.
15	N	0.8	1.2	100	--	--	2	old

[1] Naturally created (N); result of river straightening (A).
[2] Depths based on water level on May 24, 1969.
[3] Data based on visual estimates of aerial photographs of the oxbows taken during 1968, plus *in situ* observations.
[4] Scale: 1 - oxbow still connected directly to river channel
2 - floods during high water on river (1.5 - 3.0 m. above normal)
3 - floods only during exceptionally high water (more than 3.0 m. above normal)
[5] Where the actual age is not known, the age of the oxbow is said to be intermediate (int.) if sedimentation has not filled in a significant part of the basin (less than 0.25 of the basin area) and old if a significant part of the basin has been filled in by sedimentation.

concentration studied is in the lower course of the Pembina, where it flows through a broad alluvial plain(Green and Laycock 1967), deposited by periodic flooding of the Pembina and its tributary, the Paddle River.

Of the more than 30 oxbows in the region, only 15 were finally chosen for intensive investigation. These 15 oxbows are grouped into three clusters, each containing oxbows of a variety of ages including at least one newly created. These clusters were located west of Dapp (4 oxbows), west of Pibroch (7 oxbows), and along Highway 18 between Rossington and Freedom (4 oxbows) (Fig. 1).

Most of the remaining oxbows were briefly examined late in August 1969, as was a certain area along the river itself, to enable comparison with the oxbows studied intensively.

A preliminary survey was made of each oxbow studied intensively, during late May 1969, to gather some basic information on the morphometry of the lakes, and the land use in and around each lake basin. The results of the survey are given in Table 1.

II. Geology, Soils and Vegetation

The study area lies in the plain's region of Alberta, which is an undulating plateau varying in elevation from about 1100 m in the south-west to about 250 m in the north, with a regional slope toward the east. From Barrhead to Jarvie the elevation of the plateau is about 625 m. The bedrock which makes up this plateau is primarily composed of sandstones and shales from the Upper Cretaceous (Stelck

1967). During Pleistocene, the area was covered by glaciers probably originating in the Precambrian shield, which, when they retreated (*ca.* 11,000 B.P. (Bryson *et al.* 1969)), left a coating of glacial till and superglacial or periglacial lacustrine materials over central Alberta (Green and Laycock 1969 and Gravenor and Bayrock 1961).

The Pembina winds its way through these morainic deposits which, in the western parts of the Province, are Cordilleran in origin and contain a high quantity of limestone. The deposits through which the Pembina flows today are mainly alluvial sediments picked up by the river in its upper courses and deposited downstream. Much of the material is very basic, reflecting its western origin.

Soils of the area, surrounding the Pembina River valley in the Barrhead-Westlock region, belong to two orders: chernozemic (mollisols) and luvisolic (alfisols), with a scattering of regosols (entisols) and organic soils (histosols). In two recently completed, but unpublished soil surveys of the study region, the soils in the Pembina River valley are treated as a complex whose principal soils are the High Prairie series, a combination of gleyed dark grey and black chernozems (aquic boralfic argiborolls and aquic argiborolls), and Codner series, an orthic humic gleysol (haplaquoll). All these have developed on alluvial parent material (Wymuk Lindsay and Odynsky 1969 and Kjearsgaard and Peters 1969).

The soils of the region reflect aspen forest (*Populus tremuloides*) which until recently covered the area. The

Table 2. Temperature normals[1] for five selected weatherstations around the study area in degrees Centigrade

LOCATION AND ELEMENT	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	YEARLY AVERAGE
EDMONTON INTERNATIONAL AIRPORT		53° 19' N latitude				113° 35' W longitude					elevation 917 m.		
mean daily	-15.3	-12.3	-6.3	3.5	10.5	13.6	16.4	14.8	10.2	4.3	-4.9	-11.1	1.9
mean daily max.	-10.5	-7.2	-1.4	9.3	16.9	19.6	22.7	21.1	16.3	10.1	-0.7	-6.8	7.4
mean daily min.	-20.1	-17.4	-11.3	-2.4	4.1	7.6	10.1	8.4	4.0	-1.6	-9.2	-15.4	-3.6
CAMPSIE		54° 08' N latitude				114° 41' W longitude					elevation 671 m.		
mean daily	-15.4	-12.4	-6.1	3.4	9.8	13.2	15.9	14.2	9.6	4.0	-5.2	-12.3	1.6
mean daily max.	-9.2	-5.4	0.7	10.4	17.5	20.4	23.4	21.6	17.0	11.0	0.2	-6.8	8.4
mean daily min.	-21.7	-19.5	-12.9	-3.7	2.0	5.8	8.5	6.7	2.2	-3.0	-10.7	-17.9	-5.3
PEAVINE		54° 04' N latitude				114° 55' W longitude					elevation 695 m.		
mean daily	-13.9	-10.9	-4.8	4.0	10.4	13.3	16.3	14.7	10.3	4.9	-4.1	-10.8	2.4
mean daily max.	-9.4	-5.2	1.2	10.9	16.4	22.0	23.7	21.9	17.3	11.7	1.0	-6.1	8.8
mean daily min.	-18.5	16.7	-10.8	-2.9	4.4	4.6	8.7	7.4	3.3	-1.9	-9.2	-15.5	-3.9
SION		53° 55' N latitude				114° 08' W longitude					elevation 698 m.		
mean daily	-15.1	-12.1	-5.6	3.7	10.9	13.6	16.5	14.5	10.3	4.4	-4.0	-10.9	2.2
mean daily max.	-9.1	-5.6	0.4	10.4	18.6	21.3	24.3	22.2	17.6	11.2	1.3	-5.4	8.9
mean daily min.	-21.1	-18.7	-11.7	-3.1	3.2	5.9	8.6	6.7	2.9	-2.4	-10.4	-16.4	-4.6

Table 2. Continued.

LOCATION AND ELEMENT	MONTH												YEARLY AVERAGE
	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	
MEANOOK	54° 37' N latitude					113° 21' W longitude					elevation 686 m.		
mean daily	-15.2	-10.9	-5.8	3.2	10.3	14.0	16.7	15.3	10.2	5.3	-4.8	-10.1	2.3
mean daily max.	-12.3	-6.1	-0.6	8.5	16.0	19.7	22.3	20.6	15.2	9.7	-1.0	-6.9	7.1
mean daily min.	-19.7	-15.1	-9.9	-7.3	4.4	8.2	11.2	10.1	5.7	1.2	-8.6	-14.1	-2.4

[1] Nearly all of the data for this table and tables 3, 4, and 5 were supplied by the Weather Office at Edmonton International Airport, run by the Meteorological Branch of the Department of Transport. The normals, except for Edmonton International Airport and Meanook, represent the period 1931-1960. The Edmonton International Airport data represent an adjusted normal for this period, as data are available for only the last nine years. Meanook has only been in operation since 1957.

Table 3. Temperatures for 1969 for five selected weatherstations around the study area in degrees Centigrade

LOCATION AND ELEMENT	MONTH JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	YEARLY AVERAGE
ELLERSLIE[1]	53° 24' N latitude					113° 33' W longitude				elevation 694 m.			
mean daily	-27.4	-14.3	-7.9	6.1	10.4	14.2	15.4	15.6	9.7	1.8	-2.3	-7.3	1.1
mean daily max.	-24.2	-8.8	-2.3	12.2	17.9	22.2	22.6	22.8	14.9	7.1	2.9	-3.6	7.0
mean daily min.	-33.3	-19.4	-13.7	0.6	3.0	6.7	8.4	8.5	4.9	-3.6	-7.6	-11.6	-4.8
CAMPSIE	54° 08' N latitude					114° 41' W longitude				elevation 671 m.			
mean daily	-29.9	-15.5	-7.2	5.2	9.6	14.0	14.7	19.9	8.8	1.8	-3.5	-9.4	0.7
mean daily max.	-23.8	-8.5	0.2	12.3	17.4	22.2	22.2	21.6	13.8	8.1	2.6	-3.9	7.4
mean daily min.	-36.1	-22.6	-14.7	-2.0	1.8	5.7	7.2	7.1	3.8	-4.4	-9.7	-14.9	-6.6
SION	53° 55' N latitude					114° 08' W longitude				elevation 698 m.			
mean daily	-28.6	-13.8	-6.8	5.7	10.1	14.0	14.9	14.7	9.2	1.7	-2.2	-7.8	0.9
mean daily max.	-22.2	-7.3	0.3	11.8	17.6	22.2	22.3	21.7	14.2	7.5	3.5	-3.3	7.3
mean daily min.	-34.9	-20.3	-13.9	-0.5	2.6	5.8	7.5	7.6	4.2	-4.2	-8.0	-12.2	-5.6
SANGUDO-ROYDALE[2]	53° 56' N latitude					114° 37' W longitude				elevation 641 m.			
mean daily	-29.4	-15.3	-7.6	5.6	9.8	14.2	14.6	14.6	9.1	2.8*	-3.4	-9.0	0.5
mean daily max.	-23.7	-8.1	0.4	13.1	17.8	24.5	22.2	21.9	14.3	8.8*	3.1	-3.3	7.6
mean daily min.	-35.2	-22.6	-15.6	-2.1	1.8	6.1	6.9	7.2	3.7	-3.2*	-9.9	-14.7	-6.4

Table 3. Continued

LOCATION AND ELEMENT	MONTH												YEARLY AVERAGE
	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	
MEANOOK	54° 37' N latitude					113° 21' W longitude				elevation 686 m.			
mean daily	-26.9	-12.4	-5.7	6.6	10.2	14.2	15.8	15.1	9.1	1.9	-2.2	-7.1	1.6
mean daily max.	-23.6	-8.2	-0.9	11.6	15.9	20.2	21.2	20.4	12.6	5.9	1.9	3.9	6.1
mean daily min.	-30.2	-16.7	-10.5	1.6	4.3	8.1	10.4	9.7	5.6	-2.2	-6.4	-10.3	-3.1

[1] A recent agricultural weatherstation very close to the Edmonton International Airport. Data supplied by R. Longley, Department of Geography, University of Alberta.

[2] A station just south of Peavine (for which complete data was unavailable in 1969). The data for Sangudo was unavailable for October, but data from Peavine was available for that month, and is substituted. (starred temperatures are Peavine data).

dark grey soils are degrading chernozems (borolls) originally formed under grassland, but invaded by aspen, while the luvisols (boralfs) are forest soils developed under aspen. The study area is in the transition zone between aspen parkland and boreal forest (Bird and Bird 1967, Moss 1955) and consequently white spruce (*Picea glauca*), along with the aspen, is fairly common in the region.

III. Macroclimate

Alberta has a continental climate with long, cold winters and short cool summers. According to Koeppen's classification (Dfb), the plain's region of Alberta is in a cool temperate zone. This is divided into two subzones: the short, cool summer zone, and the long, cool summer zone, having a mean temperature over 10°C. for more than four months. The study region is in the latter zone (Longley 1967).

Temperature, precipitation, and presumably hours of sunshine (data only available from one station) are fairly uniform over central Alberta, mainly due to the lack of any topographic relief in the area. This is reflected in the long term normals for five weather stations surrounding the study region (see Tables 2 and 3). Generally the monthly means for the five stations are within 1°C. of each other. The mean daily temperature in the region rises above freezing in April (*ca.* 3.5°) to a high of 16.5° in July, and drops to 4.0° by October. The number of frost-free days is between 100 and 120 days (late May to early September). Precipitation over the region is generally between 450 and 500 mm per year. The greater part of this precipitation falls as rain during

Table 4. Total precipitation normals (1931 to 1960) and for 1969 in millimeters of rain for selected stations around the study area

LOCATION AND ELEMENT	MONTH												TOTAL
	JAN.	FEB	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT	NOV.	DEC	
						NORMALS							
EDMONTON INT. AIRPORT	26.7	18.8	22.9	26.9	42.7	85.3	81.5	68.6	32.0	21.3	20.6	22.1	469.4
CAMPSIE	23.6	21.1	19.1	24.1	46.7	78.7	94.7	68.8	33.0	20.3	21.6	20.8	472.7
SION	26.4	24.6	19.6	23.4	41.4	74.9	85.9	58.6	33.7	20.3	22.6	23.6	455.2
PEAVINE	28.2	21.6	20.6	21.1	46.2	82.3	94.5	81.0	33.0	21.8	16.3	21.8	488.4
MEANOOK	23.1	18.3	22.1	22.9	52.3	76.5	77.0	69.1	47.0	27.7	21.6	18.3	475.[illegible]
						1969							
EDMONTON INT. AIRPORT	27.2	17.8	9.7	16.8	31.8	25.1	91.2	84.3	96.8	25.7	19.1	16.0	461.5
ELLERSLIE	30.5	16.5	12.7	23.1	25.4	23.4	90.4	76.2	87.6	26.2	17.8	19.3	449.6
CAMPSIE	18.8	23.9	17.8	26.4	29.2	30.0	100.6	99.6	104.4	11.4	39.1	15.2	518.2
SION	26.9	22.9	16.3	43.9	41.9	24.4	109.5	137.7	123.2	14.5	29.7	12.7	604.5
SANGUDO-ROYDALE	14.0	24.1	10.2	23.4	17.8	24.4	82.6	152.9	103.9	12.7*	26.2	8.1	500.4
MEANOOK	26.7	26.7	30.7	27.2	37.3	32.0	115.6	82.3	100.1	32.5	37.6	9.9	558.8

* PEAVINE

Table 5. Sunshine data from Edmonton Industrial and International Airports, both normals and 1969, expressed in hours of bright sunshine per month

LOCATION AND ELEMENT	MONTH												TOTAL
	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	
						NORMALS (1931-1960)							
EDMONTON[1] INDUST. AIRPORT	86	119	163	221	267	251	305	269	186	157	100	78	2202.0
						(Nine year normals)							
EDMONTON INTERN'L AIRPORT	99.4	112.9	174.7	232.7	286.1	291.0	318.4	288.1	186.3	165.5	102.2	85.1	2342.4
						1969							
EDMONTON[1] INDUST. AIRPORT	86.1	111.7	182.7	222.7	310.4	325.1	328.0	344.6	139.5	176.5	113.6	90.1	2431.0
EDMONTON INTERN'L AIRPORT	103.7	111.2	162.0	210.2	305.1	309.3	336.5	333.6	140.1	169.7	113.9	91.2	2386.5

[1] Edmonton Industrial Airport: 53° 19' N latitude, 113° 35' W longitude, elevation 677 m.

June, July and August, 75 mm, 85 mm, and 70 mm respectively (see Table 4) compared with 20-25 mm per month for the rest of the year (Longley 1967).

The year of the study, 1969, was climatically unusual in two respects. First, the winter was the coldest ever recorded in the area (January temperature 11°C. below normal), but summer temperatures were very close to normal. Second, rainfall distribution was abnormal: June, normally the second wettest month, was abnormally dry (25 mm of rain approx.), while August was exceptionally wet (*ca.* 100 mm of rain); (see Table 4 for more detail).

Sunshine was also more abundant in 1969. During the growing season (May to August) there was an increase of 11-20% in the hours of sunlight, over the long term normals (Table 5). This amounts to 215-230 hours of bright sunshine, which is equivalent to 15-18 days of the growing season. This undoubtedly had a significant effect on the net plant production of the region.

The increase in the hours of bright sunlight in July and August, accompanied by normal or above normal amounts of precipitation, reflects the fact that most of the precipitation during these months seems to be the result of two storms, one in mid-July and the other in early August. These storms caused a considerable amount of oxbow flooding along the Pembina River.

IV. Oxbow Formation

Meandering is a characteristic of mature rivers which have a load so adjusted that the river is not always depositing

material, but is alternately cutting and filling its valley. Slight irregularities in the course of a river traversing its flood plain are slowly transformed into meanders by the deposition of sediment along the inside curve and the cutting away of the bank on the outside.

During the stages of high water in spring or after heavy rains, the stream cuts across the neck of the meander spur and in this way shortens its course. The arc of the meander thus abandoned is called an oxbow lake (Lobeck 1939).

The oxbow gradually becomes more separated from the parent river by the deposition of sediments in the channels which at first connect the lake to the river. In time, these connections are obliterated leaving low-lying depressions between the oxbow and the parent river. These depressions are channels through which flood waters are carried to old oxbows during periods of high water, causing periodic flooding.

The morphology of oxbow lake basins reflects their genesis. The deepest portion of the lakes are generally along the outer curves where the river was actively cutting before the meander was cut off. Generally the outer bank is much steeper than the inner; consequently, submerged and emergent communities tend to get started along the inner curves of old oxbows, where there are good deposits of sediment and large areas of shallow water.

Although oxbows are traditionally called lakes, very few meet the normal criteria used in delimiting lakes (Penfound 1953). The Pembina River oxbows, because of their size (rarely more than 50-75 m in width) and shallow basins

(Table 1), like most oxbows, might more correctly be called ponds (Reid 1961). However, for the sake of tradition and convenience they will be referred to as lakes throughout.

Methods

I. Plant Communities

The word community as used in this study is a portion of the landscape "characterized by certain species which are inconspicuous or unrepresented in other communities" (Daubenmire 1968). Although the study dealt only with plant communities, the word community alone will be used throughout as a matter of convenience.

For a community to be considered for inclusion in this study, it had to meet three sampling criteria:

(1) the community had to be dominated by natural herbaceous vegetation;

(2) the community, or at least large portions of it, had to be undisturbed, or at least appear undisturbed, by man or domestic animals;

(3) the community had to physically cover at least half the length of the oxbow lake in the zone or band in which it was found (*ca.* 0.5 ha or more).

The second criterion did not eliminate exbow communities in which small fenced off areas were used as watering places for domestic animals.

Four basic community types were recognized during this study: submerged, floating leaved, emergent, and meadow. The first three types of communities are designated after Penfound (1953) and Sculthorpe (1967); the fourth after Moss (1955).

Structure and floristic composition of the communities were examined using a series of square quadrats regularly

distributed along a baseline These quadrats were at least partially randomized by choosing the location of the first quadrat randomly, and were undoubtedly almost completely randomized while sampling submergent and floating leaved communities from a small boat. Since the aquatic and semi-aquatic communities examined during the study showed no internal periodicity in the distribution of component species, the samples gathered using systematically placed quadrats should be unbiased and amenable to standard biometric techniques (Daubenmire 1968).

Each community studied was sampled, if possible, three times throughout the growing season. These three sampling series (designated series I, II, and III) were carried out during the months of June, July and August, respectively.

While quadrat size varied directly with the size of the dominant species in a community, only three sizes were employed:

(1) 0.16 m^2 (40x40 cm) was used for all submerged and and the floating leaved communities dominated by *Potamogeton natans*;

(2) 0.25 m^2 (50x50 cm) was used for some emergent communities (dominated by *Eleocharis palustris* and *Equisetum fluviatale*) and all meadow communities;

(3) 1.0 m^2 (100x100 cm) was used on emergent communities (*Typha latifolia* and *Alisma plantago-aquatica*) and the floating leaved communities dominated by *Nuphar variegatum*.

Table 6. Cover abundance scale used to estimate species cover.

SYMBOL	PERCENTAGE CLASS	MIDPOINT
P	present only	0.01%
R	rare	0.1%
+	uncommon	0.5%
1	1-5%	3%
2	5-15%	10%
3	15-25%	20%
4	25-50%	37.5%
5	50-75%	67.5%
6	75-95%	85%
7	95-100%	97.5%

Table 7. Phenological and reproductive scales.

SYMBOL	PHENOLOGICAL STATE
B	leaf buds or herbaceous root visibly swollen and green
FOL	leaves green and of mature size except at shoot tips, etc.
YEL	leaves yellow or brown but attached and living; *not* dry/brittle
MOT	leaves mottled green/yellow/brown; population becoming dormant
DOR	leaves shed as litter in deciduous, dry/brittle or non-deciduous dormant plants; shoot growth complete and winter buds formed
	REPRODUCTIVE STATE
B	floral buds visibly swollen or partly expanded but not receptive
FL	flowers present; stamens and pistil or sporangia ripe
FR	fruits present in varying stages of maturity re: seeds
()	sterile; no spore or seed-bearing structures present blank

In each quadrat examined, each species' cover was estimated (using the scale outlined in Table 6) plus its phenology and reproductive status (using the scales outlined in Table 7), and its prevailing height. In the case of submergent and floating leaved communities, visual estimates made from the boat were supplemented or corrected by harvesting the whole quadrat.

In meadow and emergent communities, a baseline was established using landscape features as reference points within a representative and homogeneous area. If possible, a physical baseline was laid down using a steel tape. Quadrats were placed along the baseline at 1.5 m intervals on alternate sides of the line. The initial quadrat was positioned by choosing a random number from 1 to 10, and placing the upper right hand corner of the quadrat at that position along the line. Where it was not possible to lay out a physical baseline, the quadrats were positioned along an imaginary baseline, spaced five paces apart (3-4.5 m).

The number of quadrats established varied with the sampling series. During series I, five quadrats were generally used; in series II and III this was increased to 20, except for one stand dominated by *Typha latifolia* were only 15 were sampled.

Floating leaved and submergent communities were sampled from a boat using an imaginary baseline in an area which superficially appeared to be homogeneous. Quadrats were established approximately five oarstrokes (4-5 m) apart, and consisted of two types: (1) a pair of poles, 2.5 m long,

chained a fixed distance apart (40 cm) and pushed into the substrate, from which a square quadrat was estimated visually, and (2) for larger quadrats (1 m^2), four poles were used as the corners of the quadrat. In series I, generally five quadrats were established, while in series II and III 12 to 15 were sampled.

In addition to these communities studied intensively, in late August about 15 more oxbows were examined briefly, plus some stretches of the Pembina River in the study area. These cursory examinations consisted of a description of each community in the oxbow or river, its species composition, cover estimates and the average height of all species.

II. Plant Production

There were three types of measurements made in order to characterize the above substrate standing crop of the various communities studied: harvests of aboveground standing crop; chlorophyll extractions; and leaf area index determinations.

The standing crop harvests were made three times during the growing season in conjunction with the community sampling outlined above.

The number of quadrats harvested for standing crop varied with the sampling series: during series I five samples were normally harvested, while during series II and III 12 samples were harvested.

All the aboveground portions of the species which broke through the substrate inside the quadrats were harvested. After removal of all dead or inanimate material, the sample was placed in a polyethylene bag in which a number of

holes had been made. The wet weights were determined gravimetrically when the samples were "drip dry". The samples were air dried as soon as possible after harvesting (*ca*. 1 to 4 days).

During a prolonged wet period (Series I) it was difficult to dry samples dominated by *Nuphar variegatum*. However, drying occurred before a significant loss of material had occurred.

All standing crop samples were oven dried at 80° C. in a forced draught oven for 24 hr. and weighed.

In all meadow and emergent communities in Series I, all quadrats used for community data were harvested. During Series II and III every third quadrat was not harvested. The standing crop was harvested by clipping plants to within about 1-2 cm of the substrate.

Quadrats in communities dominated by *Nuphar variegatum* were harvested using a good quality, long handled pair of grass clippers.

The remaining submerged communities were harvested using a method adapted from Swindale and Curtis (1957). A dandelion rake with a wire net attached between the blade and the middle of the handle was dragged between two poles a fixed distance apart (40 cm). Since the blade of the rake was exactly 40 cm wide, this denuded a square of 0.16 m^2. After a little practice, this method worked very well in the predominantly soft sediments on which these communities occurred.

Standing crop samples harvested during Series III were

each randomly subsampled for chlorophyll determinations. This subsample (100-200 g) was cut into very small pieces and mixed. From this mixture a second subsample of five grams was randomly selected. This second subsample was placed in a Mason jar, covered with aluminum foil, containing 100 ml of 80% acetone. These jars were stored in coolers packed with ice for up to four days before the chlorophyll extraction was completed.

Chlorophyll was extracted using a Waring blender. The solution was gravity filtered, diluted to a known volume, and the amount of chlorophyll *a* and *b* present determined using a Unicam SP 600 spectrophotometer at 645 and 663 μm. The actual chlorophyll concentrations were calculated on a per liter basis, using a formula developed by Arnon (1949):

$$CL_{a+b} = 20.2 \times OD_{645} + 8.02 \times OD_{663}.$$

Leaf area index for most of the communities sampled during series II was determined using a Leaf Area Meter developed by Dr. George Woodwell, of the U.S. Atomic Energy Commission's Brookhaven National Laboratory.

The Leaf Area Meter is basically a combination of a light source and a light sensitive photomultiplier tube. An opaque object placed between the light source and light sensitive sensor blocks out some of the light getting to the sensor. A drop in light intensity is reflected in a drop in the potential produced in the sensor circuits (measured in millivolts) when compared with the potential from an unobstructed light source. The relationship between the area of opaque material blocking the light source and the drop in

potential is linear (or at least nearly so) and is given by the following equation:

$$Y = 0.145X + 50$$

where X = area of opaque material in cm^2 and Y = number of millivolts.

The leaf area in cm^2 for a subsample is found by placing it on a glass plate between the light source and sensor, and reading the millivolt scale; then the subsample is weighed immediately. The leaf area for the community may then be easily found, since the wet weight of the total sample is known.

Three standing crop samples collected from a community were each subsampled ten times. These ten subsamples were systematically chosen so that a balanced representation of the different types of plant structures present in the community were present in the samples. This insured a more accurate measure of leaf area, than a similar number of random samples (Greig-Smith 1964, Daubenmire 1968).

III. Physical Measurements

In July, four soil samples were collected for each community. These samples were regularly spaced along the baseline, and were obtained using either a bucket auger or, in deep water, an Ekman dredge. Only surface (5-10cm) samples were collected.

After the dried samples were mechanically crushed and passed through a 2 mm sieve, the Bouyoucos hydrometer method (Bouyoucos 1951) was used to determine the percentage sand, silt and clay. There was one significant modification of

the procedure; the samples were shaken for two to three hours and left to stand overnight before analysis.

The concentrations of Na^+, K^+, Ca^{++}, and Mg^{++} were determined using atomic absorption spectrophotometric methods on 1N ammonium acetate leachates of each soil sample. The method used is outlined in a publication of the Alberta Soil Survey and Department of Soil Science, University of Alberta, called *Soil Laboratory Analysis: Soil Science 421*.

Water samples were collected each time an oxbow was sampled, in a one liter polyethylene bottle. These samples were analysed the same day using a Hach Water Analysis Kit (DR-EL Engineer's Laboratory). The following were regularly analysed: hardness (carbonate, bicarbonate and total), alkalinity (calcium and magnesium), pH, sulphate, and turbidity of the water.

A Beckman RB3 Solu Bridge was used to determine the conductivity of the water samples collected from each oxbow on May 24, 1969.

A water level gauge (staff gauge), consisting of a board, was placed in each oxbow studied on May 24, 1969. The water levels in all the oxbows on that date were arbitrarily assigned a value of zero, and all subsequent water levels were expressed in terms of this arbitrary reference point.

IV. Computational Methods

Three types of analyses were performed on the community data gathered during the study: ordinations, principal component factor analysis, and cluster analysis.

Any quantitative or semi-quantitative measure of the species' abundance in a community can be used as a basis for comparing a species among communities or the communities themselves. A prominence index was chosen as the best measure of a species' importance in a community. This index is a composite index and accounts for both a species' cover and frequency (number of quadrats, out of the total, in which it was found). This prominence index has been employed by several other workers (see Stringer, 1969).

$$p = C \times \sqrt{F}$$

where p = prominence value, C = cover percentage, F = frequency as per cent. Cover class values were changed to percentages by using the midpoints of the cover classes (see Table 6).

Since most of the communities were sampled more than once, a composite species list was constructed using the data gathered during the various sampling series. The species in this composite list for each community were assigned the highest prominence value that the species had at any time during the summer; this was done to try to overcome the problem of underestimating the importance of short-lived species which might have been important contributors to the community early in the spring, but which had disappeared by late summer. For computational ease, and to eliminate a very small number of incidental species (1-2 at most) a prominence value of at least 0.5 (out of a possible 1,000), which was rounded off to one, was required for inclusion of a species in the composite community lists. These prominence

values in the composite species lists form the basis of all subsequent computations.

The indices of similarity and dissimilarity (1-index of similarity), which were used in the construction of ordinations and in the cluster analysis were calculated using Sorensen's index of similarity (Bray and Curtis 1957, Beals 1960, Greig-Smith 1964):

$$C = \frac{2w}{a+b}$$

where a = the sum of the prominence values of the first community being compared,

b = the sum of the prominence values of the second community being compared with the first,

and w = the lesser of the sums of the two sets of prominence values in common between the two communities.

These indices of similarity (and dissimilarity) were calculated using a computer program developed by Ream at the University of Wisconsin (Ream 1962) and modified slightly by John Purchase, Roger Hnatiuk, and the author (see Hnatiuk 1969 for the major changes).

These programs were run on the IBM System 360/67 computer, University of Alberta.

Ordinations were constructed using two methods: (1) the now classic method of Bray and Curtis (1957) as modified by Beals (1960), and (2) the more recently proposed method by Orloci (1966) The indices of dissimilarity used were those calculated above using Sorensen's basic equation.

Cluster analysis is a method by which, given a set of points located in a space by their relative proximities (similarities), subsets of these points can be found which are sufficiently isolated from other subsets, so that they could be recognized as discrete clusters if visualized. This method was originally developed by numerical taxonomists, but can be readily applied to the classification of plant communities (see Hnatiuk 1969, Stringer 1969). This method is of particular interest when compared with ordination techniques, since the underlying assumptions are diametrically opposed, for the ordination presupposes a continuous, the cluster analysis a discrete, non-continous pattern of distribution (Lambert and Dale 1964).

The basic cluster analysis program used is that of Carmichael (1966); see also George and Carmichael (1966) and George (1966). This program was adapted by Roger Hnatiuk (1969) to use sorted indices of similarity calculated using Ream's program (see above).

A principal component factor analysis program developed by the Educational Research Services of the University of Alberta was used to analyse the community data (Educational Research Services 1968). The type of factor analysis carried out on the data is usually called Q-factor analysis and is capable of discerning patterns of profile similarity between the communities. This means that communities with profile similarity, *i.e.* similar species composition, can be readily identified and grouped together (see Rummel 1967 and Fruchter 1954).

Results

I. Classification of Communities

Three techniques were used to group or classify the communities on the basis of their species composition: factor analysis (Table 8), cluster analysis (Table 9), and an association table (Table 10). All three techniques yielded almost identical groupings.

Factor analysis and the association table (see Methods) gave identical community groupings, which seem to be determined exclusively by the dominant species in each community (see Tables 8 and 10). The factor analysis however, has certain advantages over the association table; the factor analysis uses more information, gives a numerical measure (factor loading) of the similarity of the communities to a certain factor pattern (group), and clearly shows links between other factors in the case of a community which has species found in more than one community type.

Cluster analysis (Carmichael 1966) differs from the other two methods primarily in the placement of several submerged communities. These communities do not have a single dominant species, and are similar in composition to the submerged "understory" of the *Nuphar variegatum* dominated floating leaved communities (cluster 2, Table 9). This group of submerged communities (oxbows 1, 3 and 12) forms a satellite of cluster 2. The *Typha latifolia* community in oxbow #10 and the *Carex-Bryoid* community in oxbow #5 are satellites of cluster 4, the *Equisetum fluviatale* dominated communities, again primarily because of the

Table 8. Results of the factor analysis with axis rotated using the Quartimax method. Only factor loadings of 0.500 or higher are included.[1]

COMMUNITY	OXBOW #	FACTORS 1	2	3	4	5	6	7	8	9	10
Mixed submerged	1	0.696							0.555		
Potamogeton pectinatus	2	0.965									
Potamogeton pectinatus	4	0.993									
Potamogeton pectinatus	6	0.991									
Potamogeton pectinatus	7	0.993									
Potamogeton pectinatus	8	0.993									
Potamogeton pectinatus	11	0.996									
Mixed submerged	3								0.950		
Mixed submerged	12								0.583	0.677	
Potamogeton pectinatus-Ceratophyllum demersum	5	(0.397)									
Nuphar variegatum	3		0.991								
Nuphar variegatum	6		0.993								
Nuphar variegatum	7		0.971								
Nuphar variegatum	8		0.990								
Nuphar variegatum	9		0.880								
Potamogeton natans	4			0.988							
Potamogeton natans	8			0.985							
Potamogeton natans	12			0.980							
Equisetum fluviatale	5				0.927						
Equisetum fluviatale	8				0.943						
Equisetum fluviatale	12				0.980						

Table 8. Continued.

COMMUNITY	OXBOW #	FACTORS 1	2	3	4	5	6	7	8	9	10
Eleocharis palustris-Beckmannia zyzigachne	2					0.855					
Eleocharis palustris	8					0.964					
Eleocharis palustris	15					0.971					
Alisma plantago-aquatica	2						0.992				
Alisma plantago-aquatica	15						0.991				
Typha latifolia	10									0.702	
Carex-Acorus calamus	9							0.932			
Carex-Acorus calamus	10							0.858			
Carex-Bryoid	5							(0.437)			
Acorus calamus-Sonchus uliginosus	2										0.820

[3] Communities with the highest factor loading less than 0.500 have their highest factor loading included in brackets under the appropriate factor.

Table 9. Results of the cluster analysis (Carmichael 1966) using a resolution level of 0.200.

CLUSTER and SATELLITE	COMMUNITIES	OXBOW #
	Potamogeton pectinatus	2
	Potamogeton pectinatus	4
1	*Potamogeton pectinatus*	6
	Potamogeton pectinatus	7
	Potamogeton pectinatus	8
	Potamogeton pectinatus	11
satellite* 1	*Potamogeton pectinatus-Ceratophyllum demersum*	5
2	*Nuphar variegatum*	6
	Nuphar variegatum	7
	Nuphar variegatum	8
	Nuphar variegatum	9
	Nuphar variegatum	3
satellites of 2	Mixed submerged	1
	Mixed submerged	3
	Mixed submerged	12
	Potamogeton natans	4
3	*Potamogeton natans*	8
	Potamogeton natans	12
4	*Equisetum fluviatale*	5
	Equisetum fluviatale	8
	Equisetum fluviatale	12
satellite of 4	*Typha latifolia*	10
	Carex-Bryoid	5

Table 9. Continued.

CLUSTER and SATELLITES	COMMUNITIES	OXBOW #
5	*Alisma plantago-aquatica*	2
	Alisma plantago-aquatica	15
6	*Carex-Acorus calamus*	9
	Carex-Acorus calamus	10
7	*Eleocharis palustris-Beckmannia zyzigachne*	2
	Eleocharis palustris	8
	Eleocharis palustris	15
8	*Acorus calamus-Sonchus uliginosus*	2

* Satellites are communities not numerically similar enough to be a member of a cluster at that resolution level, but similar enough that they are linked to the cluster.

Table 10. Association Table. Dominant species in the communities studied are represented by their prominance values.

SPECIES	COMMUNITY TYPE																														
	SUBMERGED										FLOATING LEAVED								EMERGENT									MEADOW			
OXBOW #	2	4	6	7	8	11	1	3	12	5	3	6	7	8	9	4	8	12	5	8	12	2	8	15	2	15	10	9	10	5	2
Potamogeton pectinatus	975	965	919	975	835	875	76	14	63	243	13	70	183	110	29	110	83	1	99			30	7		5	20					
Potamogeton richardsonii			9		6	31	61	365	48	10	15	10	30	19	2		8						8								
Potamogeton zosteriformis			42	21				242	220		17	35	21	12	65			95													
Ceratophyllum demersum			1	20				9	80	582	32	26	18	28	158		13	82	5				15								
Potamogeton natans			9									38	26	21		871	821	763					26								
Nuphar variegatum											748	650	644	675	619																
Ranunculus circinatus	12	1				9				206																					
Eleocharis palustris																						182	296	117	2	1					22
Equisetum fluviatale																			756	436	806		7					2		30	
Typha latifolia																											252	7			
Alisma plantago-aquatica																				5		59	7		719	305	1				
Beckmannia zyzigachne																				22	13	124	2	1		2					10
Carex atherodes																				11			7				21	109	198	104	1
Carex rostrata																											18	37	209	71	
Acorus calamus																											25	54	17		275
Bryophytes																			1	205	105		1				61	25		710	2
Sonchus uliginosus																							7		10					32	181

similarity of subdominants. Both are recognized as distinct community types in the factor analysis and association table (see Tables 8, 9, and 10).

On the basis of the classification techniques used, eleven different types of communities can be discerned: three submerged (*Potamogeton pectinatus*, mixed submerged, and *Potamogeton pectinatus-Ceratophyllum demersum*); two floating leaved (*Nuphar variegatum, Potamogeton natans*); four emergent (*Equisetum fluviatale, Eleocharis palustris, Typha latifolia*, and *Alisma plantago-aquatica*); and three meadow (*Carex-Acorus calamus, Carex-Bryoid*, and *Acorus calamus-Sonchus uliginosus*).

A particular community from here on will be named by its dominant species and the oxbow number in which the community was located, *e.g.*, *Potamogeton pectinatus* #2, except for the mixed submerged communities which will be referred to as "mixed submerged".

II. Ordination

Ordinations were constructed using two different methods (Orloci 1966, and Bray and Curtis 1957) in an attempt to visually represent the relationships between the communities studied. The ordination results were very disappointing. The ordination accounting for the greatest amount of variability in the dissimilarity matrix is presented in Fig. 2. A comparison between 50 randomly chosen dissimilarities in the calculated matrix and their corresponding linear distances in the ordination revealed that about 25% of the variability is accounted for in the ordination (See Appendix E).

The four basic types of communities studied tend to overlap in the center of the ordination diagram (Fig. 2). This overlap appears to be the result of mathematical distortion introduced by projecting a multidimensional cluster of points into two dimensions. This distortion is aggravated by the low level of similarity between the communities studied. The average similarity between the stands is only 0.14 out of a possible 1.0, and 179 of the 465 similarities in the half-matrix of similarities are 0.00 indicating complete dissimilarity.

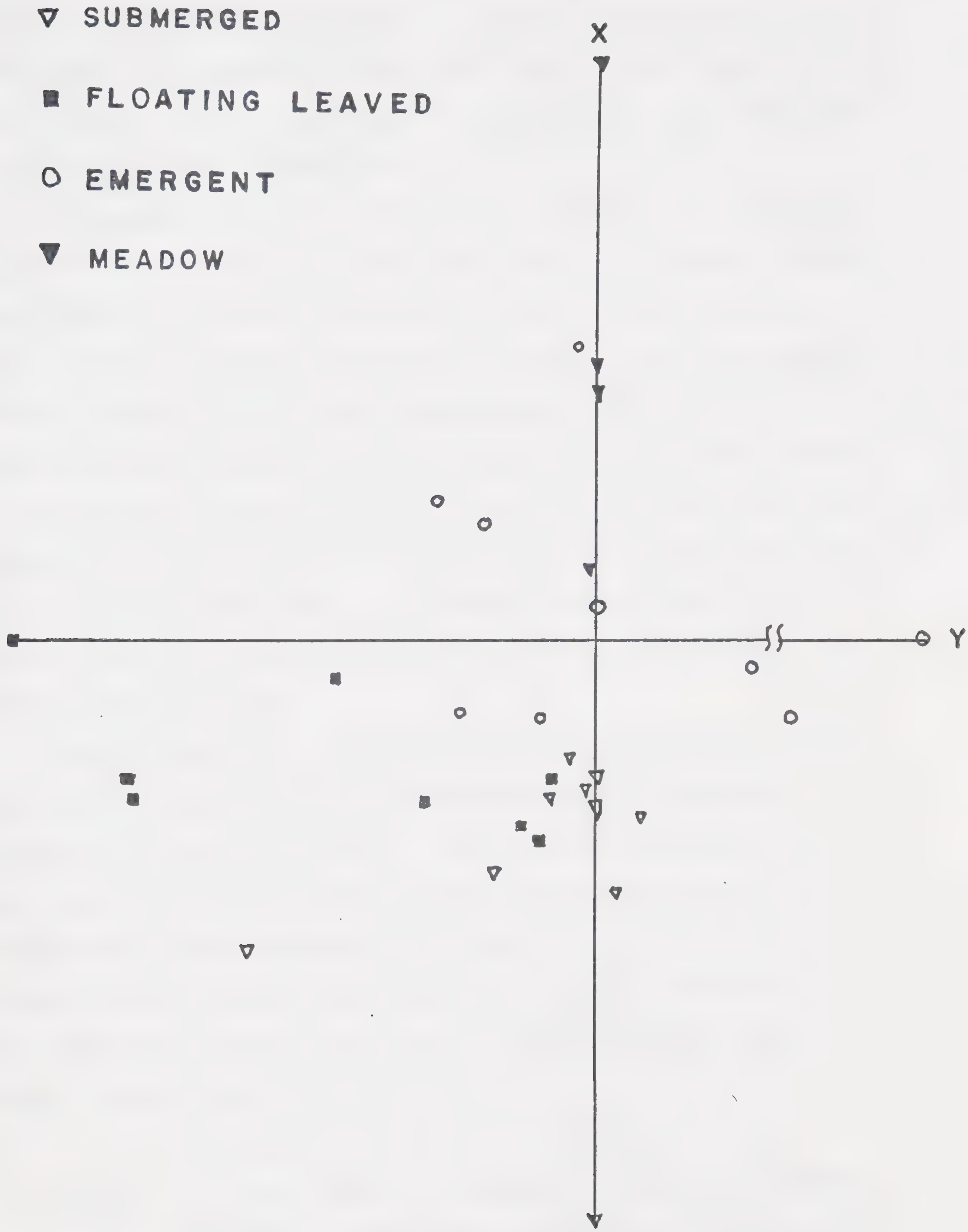
Attempts to add more dimensions (axes) to the ordination did little or nothing to improve the ordinations (see Hnatiuk 1969 for a discussion of similar problems encountered constructing ordinations).

III. Description of Community Types

Every community examined intensively is represented in Table 11 under its appropriate community type as determined by the factor analysis and association table results. This table contains a list of all species showing an average cover of more than 0.5% in the community, as averaged over the summer, plus information on the height, reproduction, and phenology of each species.

One group of species has been omitted from Table 11, small, floating, non-rooted species like *Lemna minor*, *Lemna trisulca*, and *Spirodella polyrhiza*. These species were never an intrinsic part of any of the communities, and their presence or absence depended primarily on the prevailing winds. When present they may have local cover

Figure 2. Ordination of the Pembina River oxbow plant communities.



SUBMERGED
FLOATING LEAVED
EMERGENT
MEADOW
X
Y

values approaching 60-70%, but in general rarely above 1-5%. In oxbow #10 *Spirodella polyrhiza* and *Lemna trisulca* form the only community in the open water. This oxbow is very shallow (0.3 m) and does not support any other submerged or floating leaved communities.

An examination of the species' diversity in the communities studied, in terms of the total number of species encountered during a particular sampling, indicates that there is an increase in species diversity in passing from the submerged to the floating leaved, and the emergent communities (4-5, 7, and 13-14 species respectively), followed by a slight decrease in the meadow communities (12-13 species). The emergent zone appears to have more species than these other zones, because it has species from both the submerged communities, in deeper sections of the zone, and in the shallower areas some of the meadow species.

Later stages in succession examined superficially during late August 1969 revealed that communities dominated by young *Salix* spp. (1-3 m high), with an understory of sedges and grasses, have about 40 species, while *Salix* forest communities (10-12 m high) which have a very dense canopy, have about 30-35 species. *Populus balsamifera* forests in old oxbow lake basins have a very sparse understory and appear to have only 20-25 species.

A. Submerged

There were three types of submerged communities sampled, as outlined previously. All three are generally found in the open water zone varying in depth between 1.25 and 2.0 m.

Table 11. Summary of the species composition[1], average height of the mature plants of each species, phenology and reproduction during the summer of 1969.

SPECIES	OXBOW # and COVER VALUE						AVG. HT. (m)	REPRODUCTION			PHENOLOGY		
								I[2]	II	III	I	II	III
	SUBMERGED COMMUNITIES												
	Potamogeton pectinatus												
#:	2	4	6	7	8	11							
Potamogeton pectinatus	7	6	6	6	6	5	1.3	Fl	Fr	Fr	Fol	Fol	Yel
Potamogeton richardsonii			+		+	+	1.3	Fl	Fr	Fr	Fol	Fol	Fol
Potamogeton zosteriformis			1	+			1.3	()	Fr	Fr	Fol	Fol	Fol
Ceratophyllum demersum				+			1.0	()	()	()	Fol	Fol	Fol
Ranunculus circinatus	+						2.0	Fl	Fr	Fr	Fol	Fol	Fol
Sagittaria cuneata	+						0.5	()	()	Fl	Fol	Fol	Fol
Nitella sp.						+	0.3	()	()	()	Fol	Fol	-
Myriophyllum exalbescens	+					+	1.0	()	()	()	Fol	Fol	Fol
Total number	5	4	6	3	8	6							
	Mixed Submerged												
#:	1	3	12										
Potamogeton richardsonii	1	2	1				1.3	Fr	()	-	Fol	Fol	-
Potamogeton zosteriformis		2	2				1.3	()	()	-	Fol	Fol	-
Myriophyllum exalbescens	+	2	+				1.3	()	()	-	Fol	Fol	-
Najas flexilis		1					1.3	()	()	-	Fol	Fol	-
Ceratophyllum denersum		+	2				1.3	()	()	-	Fol	Fol	-
Potamogeton pectinatus	1	+					1.3	()	()	-	Fol	Fol	-
Utricularia vulgaris	1						1.3	()	()	-	Fol	Fol	-
Total number	5	7	10										

Table 11. Continued.

SPECIES	OXBOW # and COVER VALUE					AVG. HT. (m)	REPRODUCTION I	REPRODUCTION II	REPRODUCTION III	PHENOLOGY I	PHENOLOGY II	PHENOLOGY III
Potamogeton pectinatus-Ceratophyllum demersum												
#:	5											
Potamogeton pectinatus	2					1.3	Fl	Fr	Fr	Fol	Fol	Yel
Potamogeton richardsonii	+					1.3	Fl	Fr	Fr	Fol	Fol	Fol
Ceratophyllum demersum	4					1.3	()	()	()	Fol	Fol	Yel
Ranunculus circinatus	2					1.3	Fl	Fr	Fr	Fol	Fol	Fol
Sagittaria cuneata	+					0.6	()	()	()	Fol	Fol	Fol
Total number	7											
FLOATING LEAVED COMMUNITIES												
Nuphar variegatum												
#:	3	6	7	8	9							
Nuphar variegatum	5	5	5	5	5	1.5	Fl	Fr	Fr	Fol	Fol	Fol
Potamogeton pectinatus	+	1	1	1	+	1.3	Fl	Fr	Fr	Fol	Fol	Yel
Potamogeton zosteriformis		+	+	+	1	1.3	()	Fl	Fr	Fol	Fol	Fol
Potamogeton richardsonii	+	+	+	+		1.3	Fl	Fr	Fr	Fol	Fol	Fol
Potamogeton natans		+		+		1.5	()	Fr	Fr	Fol	Fol	Fol
Myriophyllum exalbescens	1					1.3	()	()	Fr	Fol	Fol	Fol
Ceratophyllum demersum	+	+	+	+	2	1.3	()	()	()	Fol	Fol	Fol
Total number	8	11	10	11	10							
Potamogeton natans												
#:	4	8	12									
Potamogeton natans	6	6	5			1.3	Fl	Fr	Fr	Fol	Fol	-
Potamogeton pectinatus	1	1				1.0	()	()	()	Fol	Fol	-
Ceratophyllum demersum		+	1			1.0	()	()	()	Fol	Fol	-
Potamogeton zosteriformis			1			1.0	()	()	()	Fol	Fol	-
Total number	4	10	10									

Table 11. Continued.

SPECIES	OXBOW # and COVER VALUE			AVG. HT. (m)	REPRODUCTION I	II	III	PHENOLOGY I	II	III
	EMERGENT COMMUNITIES									
	Equisetum fluviatale									
#:	5	8	12							
Equisetum fluviatale	4	4	5	1.0	Fr	Fr	()	Fol	Fol	Fol
Sparganium spp.[3]	+			0.3	()	()	()	Fol	Fol	Fol
Galium trifidum		1		0.3	()	Fl	Fr	Fol	Fol	Fol
Bryophytes		3	2	-	()	()	()	Fol	Fol	Fol
Ranunculus spp.		+		0.3	()	Fl	Fr	Fol	Fol	Fol
Bidens cernua		+	+	0.3	()	()	Fl	Fol	Fol	Fol
Sium suave		+		1.0	()	()	Fl	Fol	Fol	Fol
Poa palustris		+		0.6	()	()	Fr	Fol	Fol	Fol
Total number	17	32	12							
	Eleocharis palustris									
#:	2	8	15							
Eleocharis palustris	2	2	2	1.0	Fl	Fr	Fr	Fol	Fol	Fol
Beckmannia zyzigachne	2			1.0	()	Fl	Fr	Fol	Fol	Fol
Sagittaria cuneata	1	+		0.6	()	Fr	Fr	Fol	Fol	Fol
Glyceria grandis	1			1.3	()	Fl	Fr	Fol	Fol	Fol
Mentha arvensis	+		+	0.3	()	()	Fl	Fol	Fol	Fol
Alisma plantago-aquatica	+	+		0.6	()	Fl	Fr	Fol	Fol	Fol
Phalaris arundinacea	+			1.3	()	Fl	Fr	Fol	Fol	Fol
Poa palustris	+			0.6	()	Fl	Fr	Fol	Fol	Fol
Plantago major	+			0.3	()	()	()	Fol	Fol	Fol
Bryophytes		+		-	()	()	()	Fol	Fol	Fol
Sium suave		+		1.0	()	Fl	Fr	Fol	Fol	Fol
Polyganum natans			+	0.6	()	()	()	Fol	Fol	Fol
Stellaria longipes			+	0.3	()	()	()	Fol	Fol	Fol
Total number	31	26	10							

Table 11. Continued.

SPECIES	OXBOW # and COVER VALUE		AVG. HT. (m)	REPRODUCTION I	REPRODUCTION II	REPRODUCTION III	PHENOLOGY I	PHENOLOGY II	PHENOLOGY III
	Typha latifolia								
#:	10								
Typha latifolia	3		1.5	()	()	()	Fol	Fol	Fol
Galium trifidum	+		0.3	()	Fl	Fr	Fol	Fol	Fol
Bidens cernua	+		0.3	()	()	Fl	Fol	Fol	Fol
Bryophytes	1		-	()	()	()	Fol	Fol	Fol
Marchantia sp.	1		-	Fr	Fr	Fr	Fol	Fol	Fol
Acorus calamus	+		1.0	()	Fl	Fr	Fol	Fol	Fol
Carex atherodes	+		1.0	()	Fl	Fr	Fol	Fol	Fol
Total number	26								
	Alisma plantago-aquatica								
#:	2	15							
Alisma plantago-aquatica	5	4	1.0	()	Fl	Fr	Fol	Fol	Yel
Sagittaria cuneata	2		1.0	()	()	()	Fol	Fol	Fol
Glyceria grandis	+		1.3	()	Fl	Fr	Fol	Fol	Fol
Potamogeton pectinatus		+	0.6	()	()	()	Fol	Fol	Yel
Total number	7	8							
	MEADOW COMMUNITIES								
	Carex-Acorus calamus								
#:	9	10							
Carex atherodes	2	2	1.0	()	()	()	Fol	Fol	Fol
Acorus calamus	1	+	1.0	()	()	()	Fol	Fol	Fol
Carex rostrata	1	2	1.0	()	()	()	Fol	Fol	Fol
Scutellaria galericulata	+	1	0.3	()	Fl	Fr	Fol	Fol	Fol

Table 11. Continued.

SPECIES	OXBOW # and COVER VALUE		AVG. HT. (m)	REPRODUCTION I	REPRODUCTION II	REPRODUCTION III	PHENOLOGY I	PHENOLOGY II	PHENOLOGY III
Galium trifidum	+	1	0.3	()	Fl	Fr	Fol	Fol	Fol
Calla palustris	+		0.2	()	()	()	Fol	Fol	Fol
Total number	17	15							
Carex bryoid #:	5								
Carex rostrata	1		0.6	()	()	()	Fol	Fol	Fol
Carex atherodes	1		0.6	()	()	()	Fol	Fol	Fol
Galium trifidum	+		0.3	()	Fl	Fr	Fol	Fol	Fol
Bryophytes	2		-	()	()	()	Fol	Fol	Fol
Mentha arvensis	1		0.3	()	()	Fl	Fol	Fol	Fol
Total number	22								
Acorus calamus-Sonchus uliginosus #:	2								
Sonchus uliginosus	2		1.0	()	()	Fl	Fol	Fol	Fol
Poa palustris	1		0.6	()	Fr	Fr	Fol	Fol	Fol
Galium trifidum	+		0.3	()	Fl	Fr	Fol	Fol	Fol
Acorus calamus	3		1.0	Fl	Fr	Fr	Fol	Fol	Fol
Phalaris arundinacea	+		1.3	()	Fl	Fr	Fol	Fol	Fol
Mentha arvensis	+		0.3	()	Fl	Fr	Fol	Fol	Fol
Eleocharis palustris	+		0.6	Fl	Fr	Fr	Fol	Fol	Fol
Total number	26								

[1] Species are presented using their cover values as outlined in Table 6 averaged over the whole growing season. Only species with a seasonal cover of + or higher are represented.
[2] Series I, II, and III represent the condition of the plant during June, July, and August respectively: see Table 7 for an interpretation of the reproductive and phenological symbols.
[3] *Sparganium chlorocarpum* and *eurycarpum* were not separated during series I and II.

Water more than 2.0 m in depth rarely supported any plant growth. Secchi disc readings in the lakes, taken on clear days with minimum turbidity, are generally around 2.0-2.5 m indicating that light is the limiting factor in plant distribution at these depths.

Submerged communities are generally composed of only one layer of plants extending from the substrate to the surface of the water. Dominant species in these communities show the same basic growth form, a long, narrow, flexous stem with a concentration of finely dissected or linear leaves in the upper portions of the stem. In late summer the stems are often found floating parallel to the surface. *Ranunculus circinatus* often grows out from the shore of the oxbow along the surface of the water supported by this tangle of submerged vegetation. The cover of these communities is generally very high (frequently 100%) and with the additional growth of *Ranunculus circinatus*, very dense, almost impenetrable submerged communities are often found, *e.g.*, in oxbow #2.

Potamogeton pectinatus is the dominant species in most of the submerged communities (6 out of 10) with a cover of 75-95% (Table 11). Subordinate species include: *Potamogeton richardsonii*, *Potamogeton zosteriformis*, *Ceratophyllum demersum* and *Myriophyllum exalbescens*, scattered about in fairly random clumps, rarely having a cover of more than 1%. *Ranunculus circinatus*, as already mentioned, sometimes grows along the surface.

The mixed submerged community has three dominants:

Potamogeton richardsonii, *Potamogeton zosteriformis* and *Myriophyllum exalbescens*. These three, along with several subordinate species, grow in open communities (total cover may be only 30-40%). The oxbows in which these communities are found (#1, 3, and 12) are subject to flooding. The same species are also frequently encountered in quiet stretches in the Pembina River.

Potamogeton pectinatus and *Ceratophyllum demersum* are the codominants in the submerged community in oxbow #5. This is a very dense community and resembles the *Potamogeton pectinatus* type described above, except that *Ceratophyllum demersum* is the dominant (cover 40-50%) along with *Potamogeton* (cover *ca.* 10%). *Ranunculus circinatus* was also fairly abundant in this community (cover *ca.* 10-15%).

Height of the species in these submerged communities varied directly with the depth of the water, with short, stout plants found in shallow water, while thin, flexous plants are found in deeper water. This community type was the first to die back, generally around mid-August.

B. Floating Leaved

Floating leaved communities are composed of two layers. A tall dominant whose leaves float on the surface of the water forms the upper layer. The lower or submerged layer is composed of submergent species, *e.g.*, *Potamogeton richardsonii*, *P. pectinatus*, and *Myriophyllum exalbescens*. This community is found around the outer periphery of the submerged community and ends at the beginning of the emergent community, or shore line, if no emergent community is present

in water 1.0-1.5 m deep.

Nuphar variegatum is the most common dominant of floating leaved communities with a cover of 50-75%. These plants develop from a thick rhizome growing along the surface of the substrate, from which arise clusters of leaves. These leaf clusters may cover 2-4 m^2 and are fairly regularly spaced. This regular spacing creates open areas among the clusters, in which submerged plants grow luxuriantly. The leaf petioles in *Nuphar variegatum* are generally slightly longer than the prevailing water depth (1.5-2.0 m and 1.0-1.5 m respectively).

The "understory" vegetation consists primarily of *Potamogeton pectinatus, P. zosteriformis, P. richardsonii* and *Ceratophyllum demersum* (Table 11).

The second type of floating leaved community is dominated by *Potamogeton natans*. This plant has much smaller leaves than *Nuphar variegatum* (8-9 cm in length compared to 20-25 cm), but has a higher cover value than *Nuphar variegatum* in communities which it dominates (75-95%), since plants of *Potamogeton natans* are able to grow closer together. The average height of *P. natans* was 1.25 m which was slightly greater than the prevailing water depth.

The submerged species in this floating leaved community were very sparse, and consisted mainly of *Potamogeton pectinatus, P. zosteriformis* and *Ceratophyllum demersum* (Table 11).

C. Emergent

Emergent communities grow along the water's edge from

a depth of 0.5 m to the end of the permanently waterlogged soil. These communities are generally composed of three layers. The upper, 1.0-1.5 m in height, is composed primarily of the dominant species in the community, *i.e.*, *Typha latifolia*, *Equisetum fluviatale*, *Alisma plantago-aquatica*, or *Eleocharis palustris*, and a few subordinate species, *e.g.*, *Glyceria grandis*, *Scirpus validus*, *Sium suave*, and *Phalaris arundinacea* (Talbe 11). Some of these latter species may appear as 'emergents' projecting above the general level of the upper layer, especially *Glyceria grandis* and *Scirpus validus*. The middle layer, 0.25-0.5 m in height, is composed primarily of herbs and grasses: *Bidens cernua*, *Mentha arvensis*, *Stachys palustris*, *Poa palustris*, *Polyganum coccineum*, *Stellaria longipes*, and *Gallium trifidum*. This layer is best developed in areas where there is no permanent standing water, only periodic inundation. The lower layer consists of bryoids growing along the substratum, primarily species of *Leptodictyum*, *Mnium*, and *Marchantia polymorpha*. This layer varies greatly in its extent, sometimes abundant (cover 25-30%), and in other lakes almost lacking (*ca.* 1% cover). The amount of bryoid cover seems to be inversely related to the amount of water fluctuation in the lake. Emergent communities in oxbows frequently flooded have much lower bryoid cover than do communities in stable oxbows, *e.g.*, *Equisetum fluviatale* community in oxbow #5 compared with the *Equisetum fluviatale* community in oxbow #8 (see Table 11). For the first time, there is a noticeable build up of undecomposed organic

matter in emergent communities. Often the litter has a cover of 60-70%.

Equisetum fluviatale is one of the common dominants in emergent communities. These communities are very dense (cover 40-60%) and they may have very well developed middle and lower layers in areas free of standing water. *Equisetum fluviatale* is about 1 m in height, but is subject to being blown down because of its rather weak stems. Spores are produced in the spring (May and June).

The most common subdominants in the middle layer are *Bidens cernua, Gallium trifidum, Sium suave,* and *Poa palustris.* Other species commonly found in *Equisetum fluviatale* dominated communities include *Beckmannia zyzigachne, Lemna minor, L. trisulca, Spirodella polyrhiza, Sparganium chlorocarpum* and *S. eurycarpum* (Table 11).

The second most common emergent community is dominated by *Eleocharis palustris.* These are more open communities than those dominated by *Equisetum fluviatale* with a cover in *Eleocharis* communities of only 5-15%, but they are much richer in species. The grass, *Beckmannia zyzigachne*, is also very characteristic of the upper layer and in one oxbow (#2) is as common as *Eleocharis palustris.* The dominant species in the middle layer are *Sagittaria cuneata, Mentha arvensis,* and *Alisma plantago-aquatica* (Table 11). *Glyceria grandis, Poa palustris, Polyganum natans, P. coccineum, Potamogeton pectinatus* and *Sium suave* are also characteristic members of this type of community. There is generally no bryoid cover of any note (Table 11).

The emergent community in oxbow #10 is dominated by *Typha latifolia* (cover 15-25%) which grows to a height of about 1.5 m in the main body of the community, but to a height of 2.0 m or more along the water's edge. Unlike previous communities, *Typha latifolia* grows in organic soil underlain by permafrost, or an ice lense, at a depth of about 1 m. These plants did not flower, except for a few along the outer edge, near the water.

The middle layer is again composed of *Bidens cernua* and *Gallium trifidum*, with *Carex atherodes* and *Acorus calamus* also present sporadically in open areas.

The bryoid layer is composed chiefly of *Marchantia polymorpha*. *Carex retrorsa*, *Scutellaria galericulata*, *Utricularia vulgaris* and *Hippuris vulgaris* were also present (Table 11).

Alisma plantago-aquatica dominated communities are found in deeper water than other emergent communities (0.3-1.0 m). These are also the densest emergent communities and have the fewest species (7 or 8 compared to 25-30 in many other emergent communities (Table 11)). While in the majority of emergent species most of the plant is above water level, most of *Alisma plantago-aquatica* is below water level, with only the tops of the petioles and leaf blades projecting vertically above the surface.

Alisma plantago-aquatica is generally 1.0-1.25 m in height and flowers in late June. This community is the first to die back, usually by mid-August. Common subordinate

species are *Sagittaria cuneata, Eleocharis palustris, Sparganium chlorocarpum, S. eurycarpum* and *Potamogeton pectinatus* (Table 11).

The subordinate vegetation, or lack of it, reflects the greater water depth in which these communities are found, and the density of the dominants (Table 11). In all cases where *Alisma plantago-aquatica* occurs, there is present in the shallower portion of the emergent zone a second emergent community dominated by *Eleocharis palustris* (oxbows #2 and 15).

D. Meadow

Meadow communities are found landward from the emergent types. The soils in these communities vary from being permanently to periodically waterlogged. This type of community has three layers of vegetation: an upper layer, 0.75-1.0 m dominated by sedges (*Carex rostrata* and *Carex atherodes*) and/or herbs (*Sonchus uliginosus* and *Acorus calamus*); a middle layer, 0.25-0.5 m, dominated mostly by herbs and grasses (*Scutellaria galericulata, Gallium trifidum, Mentha arvensis* and *Poa palustris*); and a usually poorly developed bryoid layer, dominated by *Leptodictym trichopodium*.

Carex atherodes, C. rostrata and *Acorus calamus* are the dominants in the most common type of meadow community studied (Table 11). *Galium trifidum, Calla palustris, Scutellaria galericulata, Epilobium glandulosum,* and *Bidens cernau* are common in the middle layer. The two dominants in this community type, *Carex rostrata* and *C. atherodes* are usually

sterile. There is also a great deal of undecomposed litter consisting primarily of last year's growth.

The *Carex*-bryoid meadow community is almost identical to the previous community type, except for the abundance of the bryoid layer of *Leptodictyum trichopodium*. *Potentilla anserina* and *Geum allepicum* are conspicuous in the drier areas.

The remaining meadow community is dominated by *Sonchus uliginosus* and *Acorus calamus* (Table 11). This community has many grasses scattered about in clumps, often appearing as emergents, *e.g.*, *Glyceria grandis*, *Phalaris arundinacea*, and *Beckmannia zyzigachne*. The middle layer is dominated by *Poa palustris*, *Mentha arvensis*, and *Eleocharis palustris*. There is no bryoid layer.

E. Shrub and Forest

Later stages of succession in oxbows lead to a series of shrub and forest communities which, although they were not studied intensively, were examined superficially.

A shrub community dominated by *Salix* spp. and *Betula pumila* var. *glandulifera* succeeds the meadow communities. These shrubs have a cover of only 40-50%, allowing a rich understory to develop. There are two understory forb-grass layers: a tall forb-grass layer (1.0-1.5 m) of *Glyceria grandis*, *Aster conspicuous*, *Aster foliaceus* , and *Urtica major*; and a lower forb-grass layer (0.25-0.75 m) of *Stellaria longipes*, *Sonchus uliginosus*, *Carex* sp., *Poa palustris*, *Galium boreale*, *Cicuta bulbifera*, *Caltha palustris*, and *Epilobium glandulosum*. A poorly developed bryoid layer,

consisting of *Marchantia polymorpha*, *Leptodictyum trichopodium*, and *Mnium* is also present.

As the willows grow in size, the predominantly meadow understory changes to one more typical of forests. These *Salix* forests are about 10 m in height and have a canopy cover of 60-75%. A shrub understory consisting mostly of *Cornus stolonifera* (cover 15-25%) is usually well developed. The herb layer is dominated by *Smilacina stellata*, *Aster conspicuous*, *Galium boreale*, *G. triflorum*, *Senecio* spp., *Rubus pubescens*, *Maianthemum canadense*, *Mitella nuda*, *Urtica major* and *Pyrola asarifolia*.

This *Salix* forest is replaced by a forest dominated by *Populus balsamifera*. The only forest trees examined had a DBH of 20-25 cm, a height of 15 m, and a canopy cover of 60-75%. This forest, like the preceding *Salix* forest, has an understory of shrubs (3-4 m in height) dominated by *Cornus stolonifera*. The herb layer is very sparse and consists of *Sonchus uliginosus*, *Anenome canadensis*, *Potentilla anserina*, *Calamagrostis neglecta*, *Rosa acicularis* and *Viburnum trilobum*. There is no bryophyte layer.

IV. Successional Patterns

The successional patterns shown by the plant communities in oxbows along the Pembina River are summarized in Fig. 3.

In quiet stretches, the river contains a number of submergent species, often locally very abundant, *e.g.*, *Potamogeton pectinatus* and *P. richardsonii*. At the water's edge, there are usually a large number of species growing: *Ranunculus gmelinii*, *Caltha natans*, *Hippuris vulgaris*,

Figure 3. Successional patterns in the oxbow lakes of the Pembina River valley.

Populus balsamnifera

Salix spp. forest

Salix-Carex-Calamagrostis

Carex spp. meadow

Sonchus uliginosus
-Acorus calamus

Eleocharis palustris

Typha lat.; Equi.
fluv; or *Alisma p-a.*

Eleocharis palustris

Nuphar variegatum or
Potamogeton natans

Potamogeton pectinatus

Caltha natans
Ranunculus spp.
Hippuris vulgaris
Scirpus microcarpus

Potamogeton richardsonii,
Potamogeton zosteriformis, and
Ceratophyllum demersum

Eleocharis palustris, *E. acicularis*, *Scirpus microcarpus*, and occasionally, *Typha latifolia* and *Equisetum fluviatale*.

When an oxbow lake is cut off from its parent river, it has already been quite extensively colonized by pioneers in at least two zones (submerged and emergent).

Succession continues in these two zones simultaneously as the oxbow begins to age. In open water the submerged community expands to areas it was previously unable to colonize because of river currents, and becomes denser. At the same time, along the lake margins, an emergent community begins to spread around the whole lake. This early emergent community is composed chiefly of *Eleocharis palustris*, *Scirpus microcarpus*, and *Sagittaria cuneata*. A third type of community may also develop on old mud flats above the water level of the new lake. This is primarily a *Salix* shrub community with a great deal of *Scirpus microcarpus*.

The next stage in succession is marked by the appearance of a new community, which begins to develop in patches in the submerged community zone, *i.e.*, a floating leaved community of either *Nuphar variegatum* or *Potamogeton natans*. The submerged communities have by this time become greatly reduced in complexity. The dominant, *Potamogeton pectinatus*, grows in extremely dense communities which virtually exclude all other species. The emergent community has also undergone a considerable change, with *Eleocharis palustris* being completely replaced by *Typha latifolia* or *Equisetum fluviatale*, or, in the deeper parts of the emergent zone, by *Alisma plantago-aquatica*.

As the oxbow continues to fill with sediment (both organic and inorganic), the submerged community is eliminated, and a floating leaved community, dominated by *Potamogeton natans* or *Nuphar variegatum*, covers the open water. The emergent band has also begun to spread in width, and a meadow community develops in areas too dry for emergents to grow. This meadow community is generally dominated by sedges (*Carex rostrata* and *C. atherodes*).

In time, the floating leaved community is eliminated and the emergent zone covers what is left of the very shallow standing water area. This is replaced by the meadow community, which is in turn, replaced by a shrub community dominated by *Salix*. This willow shrub community develops into a forest community with a typical forest herb and shrub understory. The final stage in this successional sequence observed is a forest, dominated by *Populus balsamifera*.

Succession in oxbows, especially in the early stages, is a two dimensional process. There is both intrazonal succession occurring in the open water communities and along the lake margins, and interzonal succession, in which one community type replaces another in an area with time. During the later stages, intrazonal succession ceases once mature communities are established in the submerged and emergent zones, and interzonal succession takes over.

The rate of both intrazonal and interzonal succession are very variable, and setbacks are frequent due to periodic flooding. This factor and its effects will be discussed in more detail later.

V. Standing Crop

In the communities sampled, all species die back in the fall, consequently all shoot growth represents the current year's production.

An examination of the standing crop of the various community types (Table 12) reveals that in most communities, maximum standing crop occurs in July. The only exceptions to this are the emergent communities dominated by *Equisetum fluviatale* or *Typha latifolia* which peak in August.

Mature submerged communities have a standing crop of around 200 g/m^2, while young submerged communities in newly formed oxbows have the lowest standing crop recorded, 30 g/m^2 for two year old oxbow #1, and 76 g/m^2 for ten year old oxbow #11 (Table 12). Floating leaved communities have a slightly higher average standing crop than submerged communities (221 g/m^2) while emergents had the highest shoot biomass (*ca.* 465 g/m^2). Meadow communities have a significantly lower standing crop than emergents, on the average about 327 g/m^2 (including *Eleocharis palustris-Beckmannia zyzigachne* #2), but have a higher standing crop than the submerged or floating leaved communities.

A set of one tailed "t"-tests (unpaired, with unequal variances, (Steel and Torrie 1960)) was used to compare the standing crop of different types of communities occurring in a single oxbow. A similar set of tests was also used to compare average standing crop of each of the four basic community types by pooling the maximum standing crop quadrat data for all communities of each community type (the *Eleocharis*

palustris-Beckmannia zyzigachne #2 was included in the meadow communities). The results (Table 12) show that there is a significant difference in the standing crops of the different types of communities. An example of this is found in oxbow #8, which has a *Potamogeton pectinatus* submerged community, *Potamogeton natans* and *Nuphar variegatum* floating leaved communities, and *Equisetum fluviatale* and *Eleocharis palustris* emergent communities. In July the *Potamogeton natans* and *Nuphar variegatum* communities are significantly different in standing crop, at the 95% level, from the submerged community, and likewise the emergent communities are significantly different from the floating leaved communities (Fig. 4 and Table 12).

A comparison of the pooled data for the four basic community types shows that the floating leaved communities have a significantly higher standing crop than submerged communities (at 95%), that the emergents' standing crop is significantly higher than the floating leaved (at 99%), and that meadow communities have a significantly lower standing crop than do emergent communities (at 99%). The results of the t-tests were:

(1) submerged and floating leaved community standing crop, $t = 1.674$ with $t' = 1.66$ at 95%;

(2) floating leaved and emergent community standing crop, $t = 11.054$ with $t' = 2.37$ at 99%;

(3) emergent and meadow community standing crop, $t = 4.962$ with $t' = 2.39$ at 99%.

Figure 4. Maximum standing crop plotted against succession. The line connects the means.

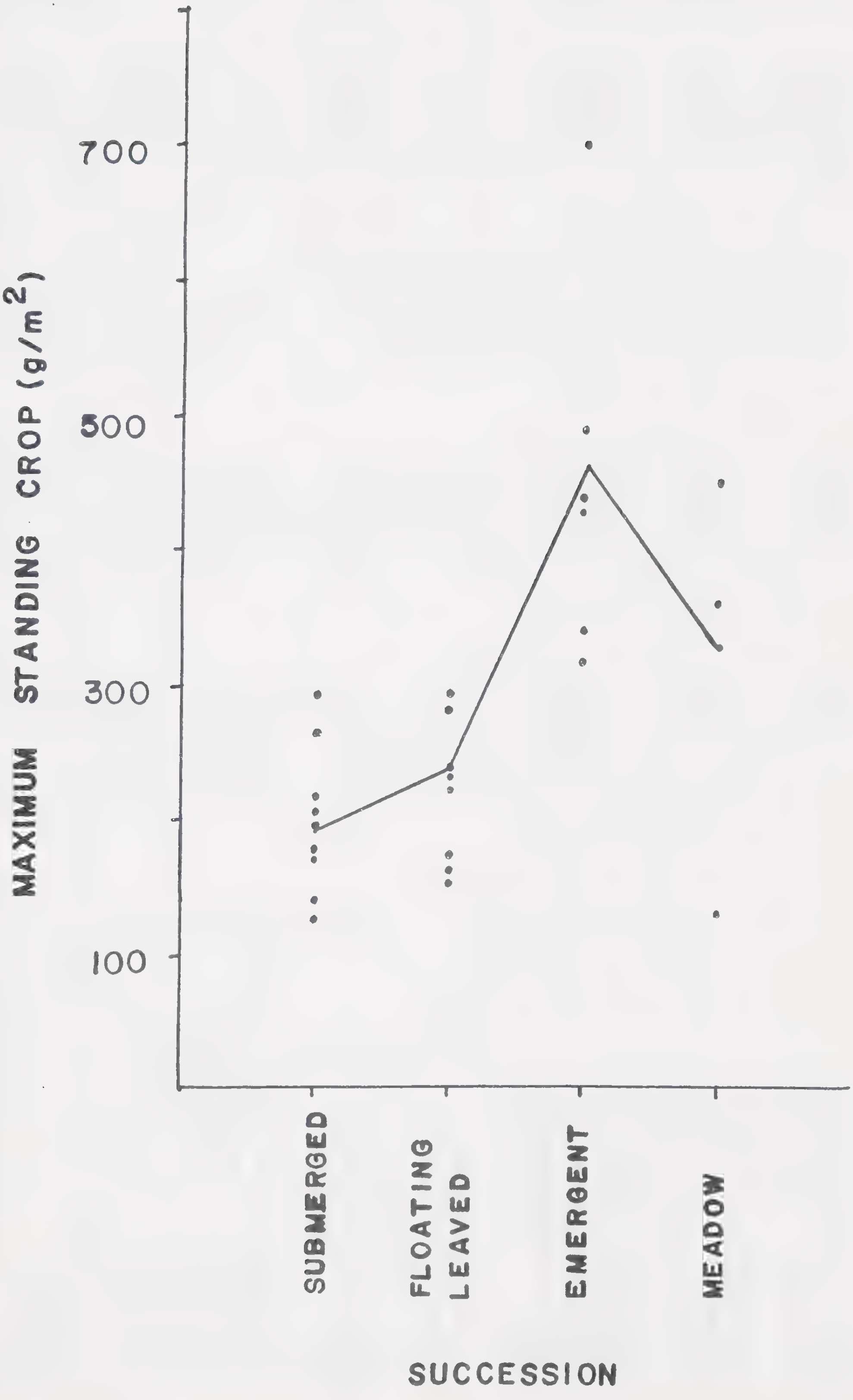

MAXIMUM STANDING CROP (g/m2)
700
500
300
100
SUBMERGED
FLOATING LEAVED
EMERGENT
MEADOW
SUCCESSION

Table 12. Standing crop summary (expressed as dry weight in g/m^2) and yield ($g/m^2/day$)[1], and leaf area index (m^2/m^2). (see note 2)

COMMUNITY	OXBOW #	SERIES[2] I Wt.±S.D.	II Wt.±S.D.	III Wt.±S.D.	YIELD	LAI m^2/m^2
Potamogeton pectinatus	2	138±95	297±101	202±56	2.972	7.0
Potamogeton pectinatus	4	170±29	179±34	- -	1.804	3.0
Potamogeton pectinatus	6	91±14	175±64	101±29	1.883	4.0
Potamogeton pectinatus	7	220±75	184±43	- -	1.955	3.5
Potamogeton pectinatus	8	129±29	144±28	- -	1.564	3.4
Potamogeton pectinatus	11	127±32	76±29	- -	1.738	1.7
Mixed submerged	1	- -	30±15	- -	0.277	-
Mixed submerged	3	- -	212±71	- -	1.985	3.1
Mixed submerged	12	198±29	130±57	- -	2.576	2.8
Potamogeton pectinatus-Ceratophyllum demersum	5	269±165	209±41	197±77	2.298	4.0
Nuphar variegatum	3	119±40	175±86*	134±54	1.636	3.7
Nuphar variegatum	6	166±43*	157±72	158±42*	1.369	2.8
Nuphar variegatum	7	101±32*	164±56	89±42	1.746	2.6
Nuphar variegatum	8	185±70	235±168*	157±73	2.67	2.5
Nuphar variegatum	9	118±35	230±76	178±69	2.472	3.5
Potamogeton natans	4	258±49*	280±57*	- -	2.857	4.7
Potamogeton natans	8	151±24	295±75*	197±91	3.352	3.7
Potamogeton natans	12	156±61	229±77*	146±53	2.271	3.1
Equisetum fluviatale	5	200±63	211±108	707±196	6.369	3.7
Equisetum fluviatale	8	312±60*	345±67*	491±83*	4.310	2.1
Equisetum fluviatale	12	312±43*	430±90*	- -	4.255	3.4

Table 12. Continued.

COMMUNITY	OXBOW #	SERIES I Wt.±S.D.	II Wt.±S.D.	III Wt.±S.D.	YIELD	LAI m^2/m^2
Eleocharis palustris-Beckmannia zyzigachne	2	112±35*	341±58*	308±56	3.280	3.4
Eleocharis palustris	8	231±46	447±99*	211±45	4.971	3.9
Eleocharis palustris	15	208±18*	- -	183±47	---	-
Alisma plantago-aquatica	2	180±44	444±91	- -	4.444	8.1
Alisma plantago-aquatica	15	52±15	- -	- -	---	-
Typha latifolia	10	181±32	271±49	322±70	2.705	3.4
Carex-Acorus calamus	9	198±74	338±114*	268±67	3.708	3.7
Carex-Acorus calamus	10	280±152	368±157	314±83	3.758	2.7
Carex-Bryoid	5	127±93	116±34*	133±92*	1.181	1.3
Acorus-Sonchus uliginosus	2	272±107*	457±109*	394±82*	4.393	4.6

[1]Daily increment is calculated by dividing the maximum standing crop by the number of days from April 15 to the date of sampling.

[2]Series I, II, and III represent samples harvested in June, July, and August respectively. Leaf areas were calculated using samples harvested during series II.

* Standing crop significantly different from that in the previous zone (beginning with the submerged communities) as shown by a t-test (unpaired, unequal variance at 95%).

These results indicate that a general trend in standing crop during succession follows this pattern: there is a general increase from submerged through floating leaved to emergent communities, then a significant drop from the emergent to the meadow communities (Fig. 4).

Daily increment follows a pattern similar to standing crop. A maximum rate of 4-6 $g/m^2/day$ is found in the emergent communities (Table 12).

VI. Leaf Area Index

Leaf area indices for the communities sampled in July are summarized in Table 12. Submerged communities generally had LAI's of about 3 to 4 except for young communities such as *Potamogeton pectinatus* #11 which had an LAI of only 1.7. *Potamogeton pectinatus* #2 had a leaf area of 6.9 m^2/m^2 due to a dense growth of *Ranunculus circinatus* as well as *Potamogeton pectinatus*.

Floating leaved communities have a leaf area, similar to submerged communities, of about 2.5-3.5 for *Nuphar variegatum* dominated communities, and 3-4 for *Potamogeton natans* dominated communities.

Except for the very dense *Alisma plantago-aquatica* #2 community with its vertically projecting leaves, emergent communities generally have a LAI very similar to that of submerged and floating leaved communities, (3-4). The *Equisetum fluviatale* community in oxbow #8 had a very low leaf area of 2.1 because of its very open growth.

Meadow communities have a LAI in the same range as previous community types (2.7, 3.7, and 4.6) for the *Carex*-

Acorus calamus and *Sonchus uliginosus-Acorus calamus* types, and 1.3 for the sparser *Carex*-Bryoid #5.

There does not appear to be any correlation between LAI and succession since leaf area remains around 3-4 for the majority of these herbaceous communities. A correlation index (Pearson's) calculated between standing crop and leaf area was barely significant at the 95% level (r=0.4177).

VII. Chlorophyll

A summary of the chlorophyll data and the correlations between chlorophyll and standing crop are given in Table 13. Chlorophyll *a* and *b* independently follow a pattern which is identical to the pattern of their total; consequently only total chlorophyll will be discussed below.

Emergent communities seem to possess the most chlorophyll, (622-2,127 mg/m^2), while floating-leaved communities have the least (293-797 mg/m^2) with submerged (240-916 mg/m^2) and meadow (542-1,414 mg/m^2) in between (Table 13).

When chlorophyll standing crop is compared to dry weight using Pearson's correlation coefficient, the results are quite variable. Some communities show a strong correlation while similar communities show little or no correlation, *e.g.*, among the emergents correlations vary from r=0.026 to r-0.828, the reason for this variability is probably the time of the year at which the samples were taken. During August many species had begun to senesce and die back, *e.g.*, *Potamogeton pectinatus*, *Alisma plantago-aquatica* and several grasses, especially *Beckmannia zyzigachne*. It is the variability caused by the senescence of these species that seems

Table 13. Chlorophyll *a*, *b*, and *a+b* (mg/m^2) and correlations (Pearson's correlation coefficient) with Dry weight (g/m^2) for communities sampled during August, 1969.

COMMUNITY	OXBOW #	CHLOROPHYLL *a* Wt.±S.D.	CHLOROPHYLL *a* r	CHLOROPHYLL *b* Wt.±S.D.	CHLOROPHYLL *b* r	CHLOROPHYLL *a+b* Wt.±S.D.	CHLOROPHYLL *a+b* r
Potamogeton pectinatus	2	485±275	0.609*	431±211	0.672*	916±485	0.645*
Potamogeton pectinatus	6	130±56	0.366	109±36	0.306	240±91	0.390
Potamogeton pectinatus-Ceratophyllum demersum	5	344±247	0.588*	281±185	0.532	630±430	0.556*
Nuphar variegatum	3	218±83	0.863*	180±64	0.790*	400±146	0.835*
Nuphar variegatum	6	209±127	0.482	204±86	0.636*	413±211	0.551
Nuphar variegatum	7	162±65	0.828*	131±51	0.800*	293±115	0.817*
Nuphar variegatum	8	355±209	0.849*	241±136	0.868*	596±334	0.885*
Nuphar variegatum	9	392±124	0.522	405±116	0.798*	797±231	0.679*
Potamogeton natans	8	295±154	0.793*	208±128	0.848*	574±279	0.828*
Potamogeton natans	12	254±97	0.728*	209±80	0.792*	463±175	0.759*
Equisetum fluviatale	5	1080±487	0.384	1058±404	0.140	2127±846	0.295
Equisetum fluviatale	8	890±180	0.766*	765±153	0.735*	1655±330	0.753*
Eleocharis palustris-Beckmannia zyzigachne	2	438±76	0.107	435±97	0.113	873±100	0.026
Eleocharis palustris	8	322±172	0.220	300±128	0.322	622±298	0.261
Eleocharis palustris	15	472±120	0.743*	416±111	0.687*	888±229	0.738*
Typha latifolia	10	427±228	0.284	418±211	0.339	845±439	0.311
Carex-Bryoid	5	301±282	0.809*	241±171	0.823*	542±448	0.821*
Carex-Acorus calamus	9	331±141	0.285	328±208	0.046	637±279	0.159
Carex-Acorus calamus	10	682±180	0.763*	637±173	0.743*	1319±1009	0.757*
Acorus-Sonchus uliginosus	2	741±242	0.713*	672±214	0.728*	1414±456	0.721*

* Significant at the 95% level (0.553).

to be responsible for the lack of correlation between chlorophyll and standing crop. For example, the two *Eleocharis palustris* communities (#2 and #8) which show very low correlations, contained significant amounts of *Beckmannia zyzigachne*, while #15, which did not, shows a high correlation coefficient of r=0.738.

There does not appear to be any relationship between leaf area and chlorophyll content (r=0.037). This reflects the fact that chlorophyll seems to be generally correlated with standing crop which changes with succession, while leaf area is not.

VIII. Soil and Water Analyses

A. Water Analyses

The ionic composition of the water in all of the oxbows is fairly similar. The water is basic with the pH ranging from 8.4 to 8.8 (Table 14). Total alkalinity of most of the lakes ranges from 90-170 ppm, and the closely related total hardness from 90-165 ppm. The alkalinity is predominantly in the form of bicarbonates. Hardness is due to the presence of Ca^{++} and Mg^{++} carbonates, with $CaCO_3$ generally accounting for 50-75% of the total hardness. Sulfate in the majority of the lakes varies from 20-30 ppm.

Oxbows #5 and #11 differ chemically, as do #13, 14 and 15 to a lesser extent, from the majority of the oxbows. Alkalinity and hardness are much higher in oxbows #5 and #11, which is reflected in their much higher conductivity values, 500 and 750 μmhos, compared to about 300 μmhos for the majority (Table 14). Oxbow #11 also has a much higher sulfate

level, 37-67 ppm.

There is a slightly higher total alkalinity and hardness found in oxbows #13, 14 and 15. This is probably due to the lack of natural vegetation around the edges of these oxbows, and a consequent increase in the run-off from adjacent fields. It may also reflect, in part, the lack of vegetation in these oxbows due to repeated flooding which eliminates, or severely reduces in size, the plant communities found in them (Oosting 1932).

Phosphate appears to be present in at least trace amounts throughout the growing season.

B. Soil Analyses

A great deal of variation is shown in the texture of the sediments, both within communities and among communities or community types. The majority of the sediments appear to be clay loams or clays, with local variations in silt and sand modifying these to silty or sandy clay loams (Table 15). This variation in sediment texture is due to the irregular deposition of sediments during periods of flooding in various areas in an oxbow. Consequently certain areas are predominantly sand, while other areas nearby are predominantly silt or clay.

Particle size below 2 mm does not appear to greatly influence plant distribution, *e.g.*, *Potamogeton pectinatus* seems to grow equally well on clay, clay loam, silty clay loam, or sandy clay loam. *Typha latifolia*, however, seems to be relegated to organic soils. Organic soils do not appear to support the growth of submerged or floating leaved

Table 14. Water Chemistry data for surface water samples taken in May, June, July and August, 1969. The data are presented in terms of the range of values found for each ion or chemical compound.

OXBOW #	TOTAL ALKALINITY (ppm of $CaCO^3$)	TOTAL HARDNESS (ppm of $CaCO^3$) and $MgCO^3$	CONDUCTIVITY (μmhos)	ORTHO-PHOSPHATE (ppm)	SULFATE (ppm)	pH	TURBIDITY (JTU)
1	110-170	130-190	350	0.0-0.5	15-25	8.2-8.7	20-100
2	90-170	95-155	400	0.1-0.6	14-35	7.5-9.9	0-32
3	110-140	90-150	360	0.4-4.8	10-38	7.9-8.9	10-30
4	80-160	90-165	250	0.4-0.7	13-30	8.0-9.4	10-120
5	110-235	110-205	500	0.3-6.5	12-20	7.5-10.5	20-50
6	90-135	90-115	300	0.2-0.4	7-20	7.8-9.2	5-70
7	90-150	110-125	330	0.2-0.5	9-11	7.4-9.3	11-42
8	90-170	80-125	330	0.2-1.4	9-25	7.6-9.4	8-50
9	110-190	95-140	280	0.5-1.2	7-38	7.4-9.0	20-30
10	110-210	140-190	440	0.9-1.7	10-45	8.0-9.3	30-45
11	160-350	160-415	750	0.2-0.3	37-67	8.0-8.4	10-32
12	110-150	100-150	300	0.4-6.5	12-40	7.5-9.5	14-60
13	140-200	115-200	310	0.4-0.8	10-30	7.9-8.6	27-130
14	140-260	145-205	350	0.9-10	14-24	7.8-8.6	27-90
15	110-200	130-255	400	0.4-0.7	10-46	7.9-9.8	20-40

Table 15. Chemical and physical analyses of sediments for each community in the fifteen oxbow lakes.

COMMUNITY	OXBOW #	TEXTURAL CLASS* (number of samples)	pH range	BASE EXCHANGE CAPACITY (meq/100gm) Na^{+}	K^{+}	Mg^{++}	Ca^{++}
Potamogeton pectinatus	2	CL(3),C(1)	7.3-7.5	0.37	1.43	7.17	23.8
Potamogeton pectinatus	4	SiCL(4)	7.7-8.0	0.09	0.96	7.17	18.8
Potamogeton pectinatus	6	CL(2),C(2)	7.6-7.8	0.22	0.84	8.20	21.3
Potamogeton pectinatus	7	CL(3),SaCL	7.6-7.7	0.24	0.92	8.20	18.8
Potamogeton pectinatus	8	C(2),SaL(1),L(1)	7.6-7.7	0.70	1.43	8.20	20.0
Potamogeton pectinatus	11	CL(2),L(1),SiL(1)	7.6-7.7	0.15	0.68	7.17	15.0
Mixed submerged	1	CL(2),L(1),SaCL(1)	7.4-7.9	0.11	0.58	6.15	17.5
Mixed submerged	3	SL(2),L(2)	7.4-7.6	0.28	1.22	9.22	21.3
Mixed submerged	12	C(4)	7.4-7.6	0.26	1.02	7.17	15.0
Potamogeton pectinatus-Ceratophyllum demersum	5	SiC(2),SiCL(1),C(1)	7.5-7.6	0.63	1.43	12.3	22.5
Open water zone[1]	10	organic	5.8-7.2	0.91	1.92	18.4	26.3
Open water zone[1]	13	SiCL(3),SiL(1)	7.8-8.0	0.15	0.67	7.17	20.0
Open water zone[1]	14	L(3),SaL(1)	7.8-8.1	0.09	0.47	0.51	13.8
Nuphar variegatum	3	CL(2),L(2)	7.3-7.4	0.33	0.95	7.17	20.0
Nuphar variegatum	6	C(4)	7.6-7.7	0.28	1.19	9.22	18.8
Nuphar variegatum	7	C(2),CL(2)	7.4-7.6	0.44	1.20	9.22	21.3
Nuphar variegatum	8	CL(3),C(1)	7.3-7.7	0.65	1.43	8.20	26.3
Nuphar variegatum	9	SaCL(3),SaL(1)	7.3-7.3	0.33	1.43	8.20	26.3
Potamogeton natans	4	SiCL(2),SiC(2)	7.6-7.8	0.13	9.95	8.20	17.5
Potamogeton natans	8	CL(3),C(1)	7.0-7.6	0.48	1.20	7.17	16.3
Potamogeton natans	12	C(4)	7.4-7.6	0.26	1.39	8.20	20.0

Table 15. Continued.

COMMUNITY	OXBOW #	TEXTURAL CLASS (number of samples)	pH range	BASE EXCHANGE CAPACITY (meq/100gm) Na^{+}	K^{+}	Mg^{++}	Ca^{++}
Equisetum fluviatale	5	SiCL(2),CL(1),SiC(1)	7.6-8.2	0.57	0.83	10.3	17.5
Equisetum fluviatale	8	C(4)	7.4-7.6	0.28	0.93	8.20	20.0
Equisetum fluviatale	12	SaCL(4)	6.6-7.2	0.04	0.45	4.10	7.5
Eleocharis palustris-Beckmannia zyzigachne	2	CL(3),L(1)	7.1-7.5	0.33	1.19	6.15	20.0
Eleocharis palustris	8	CL(3),SaCL(1)	7.7-8.0	0.22	0.59	5.12	18.8
Eleocharis palustris	15	SiCL(3),CL(1)	7.7-8.1	0.24	0.67	7.6	16.0
Alisma plantago-aquatica	2	C(2),L(1),CL(1)	7.8-	0.26	1.07	7.17	21.3
Alisma plantago-aquatica	15	SiCL(4)	7.6-7.7	0.17	1.09	6.15	18.8
Typha latifolia	10	organic	4.0-5.1	1.24	2.11	12.3	21.3
Carex-Acorus calamus	9	CL(4)	7.3-7.5	0.28	0.83	10.3	15.0
Carex-Acorus calamus	10	SaL(3),L(1)	5.3-6.6	1.07	0.60	13.3	23.8
Carex-Bryoid	5	C(4)	7.7-8.0	0.63	0.81	17.4	17.5
Acorus calamus-Sonchus uliginosus	2	L(3),CL(1)	6.8-7.2	0.26	0.84	9.22	15.0

* C-clay; L-loam; Si-silt; Sa-sand.

[1] Submerged communities absent due to flooding or edaphic factors.

communities, *e.g.*, there is no submerged community in oxbow #10 (Table 15).

The pH of the sediments is basic and usually ranges from 7.5-7.8. The only soils showing a significantly different pH are found in oxbow #10, whose organic soils have an acidic pH (4.4-6.8).

The base exchange capacity of the sediments reflect the limestone parent material from which the sediments have developed. Calcium and Magnesium ions are the most abundant, varying from 8-22 meq/100g and 4-10 meq/100g respectively. Sodium and potassium are both present, but are much less abundant; sodium has a concentration of 0.40 meq/100g, and potassium of 0.3-2 meq/100g.

There seems to be an increase in exchangeable Ca^{++} in highly organic mineral or organic soils (see *Typha latifolia* #10, Table 15). This appears to be a result of an increase in the colloidal material present in the soil. The presence of sand appears to lower the Ca^{++} exchange capacity of the soil, *e.g.*, in *Equisetum fluviatale* #5; this is presumably due to a decrease in the colloidal content of the soil.

It is not appropriate to make too many generalizations on the nature of the sediments in these oxbows, since the sediments are constantly changing due to periodic flooding. There is one trend, however, that is very evident on examination of the soils, *i.e.*, an increase in the organic matter content of the sediments with age.

Discussion

I. Classification and Ordination

All classification and ordination techniques are conceptual tools which should enable an investigator to summarize data clearly and accurately. Classification methods attempt to do this by placing the objects studied into classes or groups on the basis of common characteristics. Ordinations attempt to position the objects in a system of coordinates which will reveal their relations to all the other objects studied (Greig-Smith 1964).

Ordinations are suggested by Greig-Smith (1964) as a sound initial procedure for analysing field data, but should be abandonned if they prove inappropriate. The ordinations constructed (Fig. 2) indicate that this is an inappropriate technique due to differences in community physiognomy and floristics are too great.

Three classificatory schemes were used to group the communities: a very simple association table (Table 10) using only dominant species as indicators, cluster analysis (Table 9), and factor analysis (Table 8). The last two are methods for analysing the correlation matrix generated by comparing each community to every other community.

Cluster analysis and factor analysis are closely related; the primary difference lies in the mathematical assumptions about the entities being analysed. Cluster analysis assumes that all the entities are pure or discrete, and treats each entity as a unit mathematically, while factor analysis examines the variance of an entity, and may relate the entity

to several factors on the basis of the composition of its variance (Fruchter 1954). Cluster analysis and factor analysis should give identical results in the case of entities which are discrete, and each entity appears in only one factor. Factor analysis is the more sensitive technique, and is especially useful in analysing successional communities since the overlapping of species and other community characteristics are brought out more clearly.

The differences between factor analysis and cluster analysis (Tables 8 and 9) are mainly due to the differences in the treatment of community variance. The cluster analysis in several instances made satellites of distinct community types because of similarities in subdominants, while the factor analysis identified them as distinct groups, closely related to the groups of which they were made satellites by splitting their variances.

The classification results indicate that very simple communities with one or two overwhelmingly dominant species will yield the same groups in a simple association table and in factor analysis.

Greig-Smith (1964) considers ordination a crude factor analysis of the Q-type. He cites Dagnelie's (1960) comparison of Bray and Curtis' (1957) ordination with the results of a factor analysis on the same data, which revealed some similarities between axes and factors. In this study the results indicate that ordination is an extremely crude approximation. The best ordination accounted for 25% of the variance in the correlation matrix, while the factor analysis

accounted for about 90% (Appendix). Considering that the amount of time it would take to analyze field data by computer is the same for these techniques, factor analysis would appear to be the method of choice, because of the greater information content of the results.

II. Plant Distribution and Succession

The nature of the physical and chemical factors which control distribution of aquatic macrophytes has been a controversial subject ever since a systematic investigation of the problem was initiated at the turn of the century by Pond (1905). The controversy revolves around the role of roots in nutrient uptake in submerged plants. Many workers believe that roots serve only to anchor aquatic plants, while others maintain that they are actively engaged in nutrient uptake. Summaries of the conflict and the evidence presented on both sides can be found in Arber (1920), Bourne (1932), and Sculthorpe (1967).

The effect of this controversy on ecological studies can be seen in the relative emphasis placed on either substrate or water analysis. Water chemistry has been emphasized in many studies (Wilson 1935, Olsen 1950, Swindale and Curtis 1957, and Spence 1964, 1967); on the other hand Pond (1905), Brown (1911, 1913), Pearsall (1920, 1921), Misra (1938) and Roelofs (1944) emphasized the substrate.

Moyle (1945) examined the distribution of aquatics in Minnesota and came to the conclusion that water chemistry and substrate both influence distribution, but on a different scale. Water chemistry appears to be the most important factor influencing the general or geographic distribution of

aquatic plants, while the substrate affects the distribution of species in a particular lake or lakes with similar water chemistry.

Moyle (1945) recognize three classes of water plants on the basis of the chemical composition of the waters in which they were found: a soft water, a hard water, and an alkali or high sulfate flora. The Pembina oxbows have a water chemistry very similar to that of Moyle's hard water lakes (total alkalinity 90-150 ppm carbonate, sulfate 5-40 ppm, and pH 8.0-8.8, (Moyle (1945)) which can be seen in Table 14. Many other workers have also recognized groups of aquatic species characteristic of certain ranges of water chemistry (Wilson 1935, Olsen 1950, Swindale and Curtis 1957, and Spence 1964, 1967).

The species characteristic of the Pembina oxbows fall into two broad categories: hard water species, *e.g.*, *Potamogeton pectinatus*, *P. richardsonii*, *P. zosteriformis*, *Ceratophyllum demersum*, *Myriophyllum* spp., *Spirodella polyrhiza*, *Ranunculus circinatus* and *Acorus calamus*, and ubiquitous species, *e.g.*, *Potamogeton natans*, *Lemna minor*, *L. trisulca*, *Polyganum* spp., *Alisma plantago-aquatica*, *Typha latifolia*, *Equisetum fluviatale*, and *Carex rostrata*.

There appears to be very little correlation between plant distribution and substrate texture or chemical composition in the lakes examined. Wilson (1941) found that many aquatics do not show any marked preference for particular substrates and occur abundantly on many types of substrates, while others showed a distribution which could be correlated with substrate. Of the species common to both Wilson's lakes

and the oxbows, the majority are those which have no substrate preferences: *Potamogeton pectinatus, P. richardsonii, P. natans,* and *Ceratophyllum demersum.* However, Wilson found *Typha latifolia* growing on organic soils. Swindale and Curtis (1957) indicate that hard water species are generally found on substrates with high Ca^{++} content, high organic matter, and less sand than soft water floras, which are criteria met by most of the sediments in the Pembina oxbows (Table 15).

Other factors have been recognized besides substrate and water chemistry in controlling the distribution of aquatic plants. Diminution of light quantity and quality due to depth is one such factor (Pearsall and Hewitt 1933, Pearsall and Ullyot 1934, Westlake 1966a). In this study this is not a significant factor since the majority of the oxbows do not have regions deep enough to exclude plant establishment and growth.

Sedimentation is considered to be a very important factor in deeper lakes because the differential settling rates of various particle size classes leads to the development of distinct zones of sand, silt and clay with increasing depth (Mortimer 1949, Tadajewski 1966, Frink 1969). Oxbows, because of their narrowness and shallowness, show no such horizontal banding of sediments; instead a vertical stratification is common, since coarse material settles out faster than fines (Mortimer 1949, Ellis 1936). It is this vertical, rather than horizontal, stratification of sediments that eliminates any possible correlation between plant

disbritubion and substrate character.

Fluctuating water levels can also effect aquatic macrophyte distribution and succession (Penfound 1953). A recent study by Walker and Coupland (1968) of sloughs in Saskatchewan indicates that water chemistry and water fluctuation are the two major factors governing distribution, and that edaphic factors are relatively unimportant. Fluctuating water levels undoubtedly play a much more important role in oxbows than in the generally more stable sloughs. Oxbows, especially young ones, are very liable to flooding after a rain storm of any consequence. During the summer of 1969, all of the young oxbows flooded three times and a large number of the intermediate and some old oxbows flooded once or twice. Only oxbows #2, 8, 9 and 10 were relatively free of flood activity, but even these will flood in years with abnormally high water (personal communication from local residents).

The effects of flooding are two fold: (1) a large quantity of suspended material is deposited in the oxbow; (2) the light penetration during flooding and immediately after is effectively reduced to nil (Secchi disc readings during flooding and immediately after were only in the range of 1-4 cm).

Silt deposition due to three days of flooding in June was estimated for oxbows #13 and 14, to be 3-4 cm. This was enough to completely bury all the submerged vegetation, and subsequent flooding in July and August prevented the recolonization of these oxbows. The effects of silt deposition on aquatic plants and its retarding effects on succession have

been reported by Edwards (1969) for South African rivers. Edwards concludes that the paucity of submerged and floating leaved aquatics is due to the frequency of flash floods and the resultant silt deposition. Edwards (1969), however, maintains that the deposition of silt has one compensation for aquatic plants, an increase in the dissolved solids in the water. Ellis (1936) was unable to demonstrate such an increase for similar rivers after floods.

In intermediate oxbows, flooding does not result in the deposition of large silt loads. In these lakes, reduction of light, rather than a physical burying of the communities, is the major result of flooding. Light reduction, even after flooding ceases, can be quite sever due to the continued suspension of fine particles in the water column. Ellis (1936), has shown experimentally that after four days of settling enough material remains suspended to reduce light to one millionth of surface intensity at 1.5 m (this would normally occur at 15 m, see also Edwards 1969). During this study, field observations revealed that it takes from six to eight days after flooding ceases before the majority of the material in the water has settled (as revealed by near-normal Secchi disc readings), and that floods generally last from two to three days. Plants, then, which are able to survive in these oxbows must be able to tolerate low light intensity for periods of up to 7-8 days.

Wilson (1941) recorded the depths and light intensities at which species grew in Wisconsin lakes. His study revealed that *Potamogeton richardsonii, Ceratophyllum demersum,* and

Najas flexilis could tolerate much lower light conditions than *Potamogeton pectinatus*. This could explain why these shade tolerant species are more common in certain oxbows subject to flooding (#1, 3, 5 and 12), and why these are common understory species in floating leaved communities (Table 11). Bourne (1932) has also shown that *Potamogeton pectinatus* cannot survive under low light conditions and is consequently eliminated from turbid water.

Bernatowicz (1966) has experimentally demonstrated that many emergents are adversely effected by shading. The most shade tolerant species in his study was *Equisetum limosum*. The shading produced by flooding may in part explain the diversity of emergents found in Pembina oxbows.

Field observations reveal that *Typha latifolia* and *Alisma plantago-aquatica* are severely set back or killed by submergence for any prolonged period of time. Bedish (1967) reports that *Typha latifolia* cannot tolerate water beyond 0.25 m and that its seeds need light to germinate, which does not make it a favored species in areas of repeated flooding. Before flooding in June, oxbow #15 had communities dominated by *Alisma plantago-aquatica* and *Eleocharis palustris* (Table 11). After flooding the permanent water level of the lake was raised by 0.75-1.0 m which resulted in the death of the *Alisma plantago-aquatica*, but the *Eleocharis palustris* continued to grow and in August the plants were projecting about 0.25 m above water. Similar observations have been reported for *Eleocharis palustris* growing along flood plains by Byallovich (1969).

The information above would suggest that *Typha latifolia* and *Alisma plantago-aquatica* should be restricted to stable oxbows, and that *Equisetum fluviatale* (presuming it has as high a shade tolerance as the closely related *Equisetum limosum*) and *Eleocharis palustris* would be found in lakes subject to periodic flooding. This is generally the situation. However, *Eleocharis palustris* seems unable to coexist with *Equisetum fluviatale* or *Typha latifolia*, and is usually found associated with *Alisma plantago-aquatica*, but only in the shallower portions of the emergent zone.

The effects of flooding on standing crop can be seen in Table 12. For example, *Nuphar variegatum* communities in oxbows #6 and 7 when sampled in July (II) had very similar standing crops (157 and 164 g/m^2) but in August (III) these were 158 and 89 g/m^2 respectively. Oxbow #6 was sampled before the August flood, while oxbow #7 was sampled afterwards. Flooding can have much more drastic effects on standing crop, *e.g.*, in August it completely destroyed the *Equisetum fluviatale* in oxbow #12 (Table 12).

Flooding is generally considered to have a strong positive effect on succession, due to an increase in the sedimentation rate, as long as it is not too severe to prevent colonization and ecesis (Pearsall 1920, Penfound 1953, Spence 1967, Thomas and Bromley 1968, and Edwards 1969, *inter alia*), and will also determine which pioneer species can become established in a lake. Sedimentation also effects later successional stages. Sediments in lakes subject to flooding are rich in bases (Table 15), and consequently there is usually

a complete decomposition of organic matter (Pearsall 1921). However, in oxbows with little flooding an organic soil may develop due to the low level of base rich silts and clays, *e.g.*, oxbow #10. The build up of organic matter has a marked effect on the pH of the substrate, *e.g.*, in oxbow #10 the soil pH is usually acidic and can be as low as 4.4. Misra (1938) has noted that with succession, as long as organic matter decomposes, there is no marked change in the pH of the substrate (see Table 15). This substrate difference correlates with the distribution of *Typha latifolia* (organic soils) and *Alisma plantago-aquatica* (mineral soils) in stable oxbows.

Although flooding does vast amounts of damage to most aquatic communities, it does have beneficial effects; it keeps the oxbows full of water and provides a further nutrient input. The annual rate of water evaporation from lakes in the Westlock region is about 625 mm (Longley 1968), while the annual rainfall is only 470-480 mm. Since oxbow lakes have basins rarely exceeding the standing water area, there is a net loss of water of 135-145 mm yearly. Actual measurements of water levels during the summer (May 24, 1969 to mid Aug.) in oxbows that did not flood indicate a net loss of 150-400 mm of water.

Floods not only refill these oxbows periodically, but in effect rejuvenate them, by temporarily reversing successional trends (Lippert and Jameson 1964). Succession consequently progresses not linearly, but rythmically, with four steps forward followed by three steps backward.

After the meadow stage, succession is controlled by the height of the permanent water table. Accompanying a gradual drop in the water table is a change from a meadow to a shrub community (*Salix*). Old oxbow basins, however, always remain wetter than surrounding areas and, consequently, *Populus balsmifera*, not *Populus tremuloides* dominates the forests in these old depressions.

The rate of succession in oxbow lakes is very hard to accurately estimate. Oxbows cut off from the Pembina before 1900 (communication from local residents), *e.g.*, #'s 3, 6, 7, and 12, have communities very similar and at the same stage of development as oxbows cut off only 10-11 years ago, *e.g.*, #4 and #11. This reflects an increase in the rate of sedimentation due to an increase in flooding since 1900 or later. Using estimates of sedimentation rates based on observations during the summer of 1969 in oxbows not subject to severe flooding (1-3 cm/yr on the average) and assuming an average depth of 3 m when the oxbow came into existence, it would take from 100 to 300 years for an oxbow formed before 1900 to fill in completely, *i.e.*, to go from an early submerged to the meadow stage in succession (Fig. 3). For oxbows cut off 10-11 years ago this would take only 25-75 years since they are subject to more severe flooding.

Cores from willow and poplar forests suggest that it takes at least 80-100 years for a mature forest to replace the meadow stage in succession.

It must be emphasized that the times outlined above are mostly based on conjecture and at best indicate the order of

magnitude required for major stages in the successional sequence. However, there is good evidence to suggest at least a sixfold increase in the rate in early stages of succession since 1900.

III. Hydrarch Succession in Alberta

The successional sequence outlined in Fig. 3 differs from all those previously described in the literature on Alberta, not in its general trends, but in the species composition of the individual communities.

Raup (1934, 1935) described zonation patterns in a variety of northern Alberta lakes, and many of his early stages are similar to those found in the Pembina oxbows. Bird (1930, 1961) outlines a general successional sequence for Parkland zone sloughs which is also very similar, especially in the later stages. Bird's sequence does not describe the submerged communities in any detail, and has no floating leaved stage.

Early work on aquatic and semi-aquatic plants in Alberta by Lewis and co-workers (Lewis and Dowding 1926 and Lewis *et al.* 1928) was continued by Moss (1953). This work is summarized by Moss (1955) who outlines a successional scheme for lakes in central Alberta: aquatics→*Typha-scirpus*→*Scolochloa-Carex atherodes*→*Glyceria-Carex* spp.→*Salix* spp.→*Populus balsamifera*. This scheme has certain similarities with that outlined in Fig. 3, but the dominants in early stages are different. The differences among the sequences described by Raup (1934, 1935), Lewis *et al.* (1928) and Moss (1955) are most likely due to the effects of periodic

flooding, which has eliminated all species not capable of tolerating floods in the Pembina oxbows.

Recently a number of investigations of aquatic problems in Central Alberta have touched on the distribution and floristic composition of aquatic communities (Bozniak 1966, Johnston 1966, Daborn 1969, and Wheelock 1969). These studies reveal that in lakes whose water chemistry is similar to that of the oxbows, the same species of aquatic and semi-aquatic plants are sometimes found.

IV. Productivity

No attempt was made to measure photosynthetic or respiratory rates during this study. However, an estimate of net shoot production can be made from the standing crop values, since all standing crop represents this year's growth and very little is lost to herbivores (Westlake 1965). Attempts were made to examine two of the most important factors governing productivity: chlorophyll content and structure, as reflected by community height, number of photosynthetic layers of vegetation, and leaf area index.

A. Standing Crop

Data from previous studies of aquatic macrophytes reveal that submerged communities generally have a maximum standing crop of 175-240 g/m^2 in the case of *Myriophyllum* (Lind and Cottam 1969, Forsberg 1959), 129 g/m^2 for *Potamogeton crispus* (Ikusima 1965), 120 g/m^2 for *Potamogeton pectinatus* (Westlake 1961), 500-700 g/m^2 for *Ceratophyllum demersum* (Forsberg 1960), and 202 g/m^2 for submerged plants in Lake Mendota (Wilson 1935). The maximum standing crop for submerged communities in this

study was *ca.* 200 g/m^2, which appears to be about average.

There have been very few measurements of the standing crop of floating leaved communities. Bray (1960) records a shoot biomass of 110 g/m^2 for *Nymphaea odorata* in Minnesota, which is considerably lower than the average maximum standing crop of 220 g/m^2 for floating leaved communities found in these oxbows.

Emergent communities, however, have been thoroughly examined by many workers: Penfound (1956) reports 1,527 g/m^2, Bray (1960) 1,400 g/m^2, and Kvet *et al.* (1969) 1,620 g/m^2 for *Typha latifolia.* Bray (1960) reports a standing crop of 320 g/m^2 for *Equisetum fluviatale,* and Westlake (1966b) 656 g/m^2 and 673 g/m^2 for *Glyceria grandis.* Similar results are reported for a number of other emergent communities, especially those dominated by *Phragmites communis*: Bray *et al.* (1959); Krasovsky (1962); Buttery and Lambert (1965); Kvet *et al.* (1969); Bernatowicz *et al.* (1968); and Pearsall and Gorham (1956).

The standing crop of the four types of emergent communities examined fall into the lower range of the values reported in the literature. The *Typha latifolia* #10 community has a standing crop of only 20-25% of that usually reported. This may be because of autotoxic feedback (McNaughton 1968) or the presence of an ice lens, since the community did not appear very vigorous and never flowered. The *Equisetum fluviatale, Eleocharis palustris* and *Alisma plantago-aquatica* all appear to have a standing crop (about 450 g/m^2) lower than that for grass dominated emergent

communities, but similar to that of the *Equisetum fluviatale* recorded by Bray (1960).

Meadow communities have been examined by Bray (1959) who reports a standing crop of 480 g/m² and 410 g/m² for *Carex lasiocarpa* and *C. lasiocarpa-Calamagrostis canadensis* communities respectively. Pilat (1967) reports standing crops of 515, 425, and 400 g/m² for various meadow communities, and Jakrlova (1967) gives standing crops of 400-550 g/m² on the average, but as low as 250 g/m², for a number of meadow communities subject to flooding. Pearsall and Gorham (1956) and Getz (1960) give data for meadows in which *Carex rostrata* is one of the dominants (420 and 465±121 g/m² respectively).

The standing crops of meadow communities in this study are slightly lower than the literature values, about 350 g/m² for sedge dominated communities and about 460 g/m² for the herbaceous community.

No actual measurements of root or rhizome standing crop were made, but data from the literature indicate that root/shoot ratios, although they fluctuate, are fairly stable (Westlake 1968, Szczepanski 1969) in aquatic plants.

Submerged plants generally have a root standing crop of 0-10% of the total biomass (Westlake 1963, Edwards and Owens 1960). Floating leaved plants have rhizomes that account for 50-80% of the total biomass (*Nuphar lutea* and *Nuphar pumilum*); *Alisma plantago-aquatica, Equisetum fluviatale* and *Typha latifolia* have roots or rhizomes that account for 40%, 40-85% and 40-55% of their total biomasses

respectively (Westlake 1968, Fiala *et al.* 1968). Meadow species, *e.g.*, *Carex* spp. and *Acorus calamus* have underground organs that account for 20-60% of the total biomass, but generally around 30% (Westlake 1963, 1968, Bray, 1963, Evodokimova and Grishina 1968). The age of these rhizomes has been determined experimentally to be between two and three years (Westlake 1968) with an average of just under two years.

Based upon the above studies, root production in submerged and *Potamogeton natans* communities on an annual basis is about 5% of the total biomass. Similarly, for floating leaved communities (*Nuphar variegatum*), emergent and meadow communities, there is an annual root production which represents approximately 25-40%, 20-40% and 10-30% of the biomass respectively. This pattern follows the pattern of shoot standing crop, and would increase the differences in total biomass between the various successional stages, as previously outlined in Fig. 4. The average annual production (below- and aboveground) for the summer of 1969 would be around 210 g/m^2 for submerged, 285-600 g/m^2 for floating leaved, 610-1,380 g/m^2 for emergents and 425-612 g/m^2 for meadow communities, but more productive communities greatly exceed these limits, *e.g.*, *Equisetum fluviatale* #5 and *Acorus calamus*-*Sonchus uliginosus* #2 having 940-2,120 g/m^2 and 560-805 g/m^2 respectively.

This increase in annual net production from submerged to emergent, and the decrease from emergent to meadow has been previously postulated by Penfound (1956) and Westlake (1963)

on the basis of fragmentary evidence from a number of studies. Bernatowicz *et al.* (1968) give a series of wet weight measurements at various depths with a similar pattern, but they did not sample meadow communities.

B. Leaf Area

Recent interest in leaf area measurement has stimulated a review article (Marshall 1968) and a number of comparative evaluations of technique (Ondok 1968, Jones 1968). Ondok (1968) compared a photoelectric planimeter, very similar to the one used in this study, to other methods and concluded that the photoelectric planimeter deviated only about 1.5% from the standard for large samples.

Ikusima (1965) reported the LAI of two submerged communities: *Vallesneria asiatica* with 2.3 and *Potamogeton crispus* with 4.2. Kvet *et al.* (1969) did a detailed study of the leaf area development in *Typha latifolia* and *Phragmites communis* and reported maximum LAI's of *ca.* 3 and 6-7 respectively, which occurred in July although both had similar standing crops.

Studies by Golley (1965) on broomsedge reveal that maximum leaf area occurs along with maximum standing crop in July. Bazzaz and Bliss (unpublished) followed leaf area in a deciduous forest understory and found that maximum leaf area occurred in May or June, slightly after maximum standing crop had been reached. Jones (1968) examined heathland communities in which leaf area increased during periods of active growth and then declined when growth ceases. These studies indicate that July leaf area

measurements for the oxbow communities represent maximum leaf areas, or very close to maximum leaf areas, since the majority of the communities had their maximum standing crop in July (Table 12).

Agricultural workers (Donald 1961, Brougham 1963) have reported leaf area indices of 3 to 7 and 9 to 12 for herbaceous and pasture crops respectively. Chang (1968) states that most crops have LAI's of between 2 and 6, but that plants with vertical foliage can have much higher leaf areas (9 to 12 as in wheat). Similar results have been reported by Aruga and Monsi (1963) for natural communities.

Experimental studies by agricultural workers show that several factors influence leaf area: radiation intensity, patterns of leaf development and projection, and the density of the community (Watson 1952, Donald 1961, Chang 1968).

The leaf areas (Table 12) of the communities studied were all very similar, about 3 to 4, except for a small number of communities that were either poorly developed or had vertically projecting leaves, or were unusually dense due to the growth of *Ranunculus circinatus*. There seems to be no general change in leaf area in these early successional stages, although this will undoubtedly occur once trees and shrubs become established (Aruga and Monsi 1963). Leaf area *per se* does not seem to be a primary factor in determining a community's annual production, nor a good estimate of standing crop.

C. Chlorophyll

The chlorophyll content of the photosynthetic tissue

has also been cited as a key factor controlling productivity (Odum 1959, Odum *et al.* 1958, Aruga and Monsi 1963). Three factors must be considered when interpreting chlorophyll data: the amount of chlorophyll per unit area, its vertical distribution, and the physiological state of the chlorophyll. It is presumed that the bulk of the chlorophyll was active in the plants sampled.

The total chlorophyll of a *Nuphar variegatum* community is given as 440 mg/m^2 by Jahnke and Lawrence (1965). Bray (1960) gives chlorophyll data for a number of communities in a hydrarch successional sequence: *Nymphaea odorata*, 350 mg/m^2; *Equisetum fluviatale*, 960 mg/m^2; *Carex lasiocarpa*, 1,270 mg/m^2; and *Carex lasiocarpa-Calamagrostis canadensis*, 1,300 mg/m^2. Bray (1960) also gives data (4,650 mg/m^2) for a *Typha* community. Aruga and Monsi (1963) give a total chlorophyll content of 4,090 mg/m^2 for *Phragmites communis*. Chlorophyll values for periodically inundated meadow communities range from 440-2,940 mg/m^2 according to Pilat (1967).

In the present study submerged communities had a chlorophyll content of 240-916 mg/m^2, while the floating leaved communities had between 300-800 mg/m^2 (generally about 400 mg/m^2). *Equisetum fluviatale* had a high chlorophyll content of 1,600-2,100 mg/m^2, but total chlorophyll was only about 850 mg/m^2 for *Eleocharis palustris* and *Typha latifolia*. The meadow communities have values very similar to those reported by Bray (1960) and Pilat (1967), and ranged from about 550-1,400 mg/m^2. Aruga and Monsi (1963) give chlorophyll concentrations of about 1,000-4,000 mg/m^2 for terrestial herb

communities. It would appear that submerged and floating leaved communities contain less chlorophyll than terrestial communities, but emergent and meadow communities have chlorophyll values in the same range as most terrestial herbaceous communities.

The maximum chlorophyll content of a natural community normally occurs around the time of maximum standing crop in either July or August (Golley 1965, Ovington and Lawrence 1967) or slightly after the maximum standing crop in understory herbs (Bazzaz and Bliss, unpublished). The August chlorophyll content was probably below the maximum standing crop, except for the *Equisetum fluviatale* and *Typha latifolia* communities. This partially accounts for their being lower than the literature values, as does the much lower standing crops of these communities.

It has been reported by many workers that there is a seasonal variation in the amount of chlorophyll per unit weight (Brougham 1963, Golley 1965, and Ovington and Lawrence 1967). However, there is generally a good correlation between the standing crop and chlorophyll at any one time during the growing season (Bray 1960, Tieszen and Johnson 1968, Bliss 1969). The correlation coefficients calculated between standing crop and chlorophyll for Pembina oxbow communities show a large range of values, from about 0.00 to 0.88 (Table 12).

The reasons for the variation between chlorophyll and standing crop are probably (1) experimental error (see Bray 1960 for a discussion of the possible errors in chlorophyll

estimation), (2) phenological changes occurring in many of the plants in mid-August, and (3) flooding, which can greatly effect the chlorophyll concentrations (Pilat 1967). Pilat (1967) found that the fluctuation of chlorophyll was more pronounced than that of dry matter production in communities subject to flooding and that a correlation between standing crop and chlorophyll existed during normal growth conditions, but not after flooding.

Bray (1960) found a significant difference in the chlorophyll content of various communities in a hydrarch successional sequence. The data from the oxbow communities seem to indicate a definite pattern: submerged communities have more chlorophyll than floating leaved communities, which have less than emergents, as do the meadow communities. This pattern is similar, but not identical, to that found for biomass. The main difference lies in the fact that the chlorophyll content of submerged communities is higher than that of floating leaved, while the reverse is true of their biomass.

D. General Discussion

The lower standing crop, and, by extension, productivity, of submerged and floating leaved communities is due to several factors. The water reflects and absorbs some of the incident radiation which could be utilized by aerial plants. Since submerged communities and a great part of many floating leaved communities are vertically suspended in the water column, a large part of the effective biomass will be poorly illuminated, and its respiration will depress the net photosynthesis of the community (Westlake 1963). Problems with

carbon dioxide and bicarbonate exchange due to slow diffusion rates in water may also reduce productivity. Flooding reduces the productivity not only during periods of high water due to shading, but consequently because of the layer of silt and clay deposited on the photsynthetic tissues.

Emergents, in most respects, have the best of both worlds: gaseous exchange of carbon dioxide and direct sunlight, plus an adequate supply of water and nutrients (Pearsall 1950). This may account for their much greater productivity when compared with adjacent submerged and meadow communities (Odum 1969).

Besides these environmental parameters, productivity is also greatly influenced by the structure and chlorophyll content of the community. Leaf area index cannot be a principal factor which governs production in these communities, since it remains fairly constant, while productivity can vary threefold. An increase in the structure of communities occurs during succession: submerged communities have only one layer of photosynthetic tissue, floating leaved communities two layers, emergents three, and meadow two or three layers, yet there is little change in leaf area index. The depth of the photosynthetic crown of these communities also differs: submerged 20 cm, floating leaved 20 cm, emergent 100-150 cm, and meadow 75-100 cm. Bray (1960) found a correlation between an increase in height and chlorophyll content which reflected an increase in the structure of the communities and also its productivity. This same pattern is evident from these data: an increase in height is

accompanied by an increase in chlorophyll and community structure. An increase in the productivity of a community results, due to this increase in height and structure, since there is a greater chance of the light entering a community being intercepted (Saeki and Kuroiwa 1959, Saeki 1960, Monsi 1960, Jahnke and Lawrence 1965, Tooming 1967, *inter alia*).

The increase in annual production with succession does not appear to a smooth progression, but rather a series of steps (Table 12). This stepwise progression is linked to the physical changes that result in an area as a result of succession. The gradual filling in of the oxbow enables new life forms to become established as the water depth decreases. These new life forms are generally taller and more massive, since they are able to make more efficient use of their environment or because the environment has been made less rigourous by previous stages. The more efficient utilization of minerals, light and CO_2 accompanied by an increase in height, structure, and chlorophyll content enables more energy to be trapped by successive stages. As a result, the establishment of a new life form leads to a sudden increase or decrease in annual production (Odum 1960). A decrease in production may occur, if a new life form invades an area that has become more rigorous as a result of the activity of previous stages. The meadow community which replaces the emergent community in an oxbow is less productive because it does not have the ready water and nutrient supply of the emergents and is

consequently a less productive life form (Odum 1969).

That a change in life form rather than an increase in species diversity, which follows the same pattern as annual production, is the primary factor responsible for the step-wise increase in annual production accompanying succession can be clearly seen by examining the *Equisetum fluviatale* communities in oxbows #'s 5, 8 and 12 (Table 11) and their standing crops (Table 12). In July these three communities had aboveground standing crops of 511, 345 and 430 g/m^2 respectively; however, these communities were quite different in their species diversity *ca.* 17, 32, and 12 species respectively (see also Golley and Gentry 1965 and Odum 1960).

An increase in the stability of a community with succession appears to be due to an increase in the standing crop of the community resulting from a change in life forms. An increase in the size of the dominants, which enables them to store large quantities of energy, allows them to survive periods of unfavourable conditions more readily than smaller sub-dominants. When a community is subject to flooding all of the smaller species are eliminated before the dominants. The dominants provide community stability during the early stages of succession. Species diversity does not reflect community stability, but environmental stability.

Summary

1. A series of oxbow lakes cut off by the Pembina river were examined to determine the successional sequence and productivity, as reflected in the standing crops of the various communities.

2. Chemical and physical data were gathered to determine their influence on plant establishment, distribution, and succession.

3. Eleven communities were recognized as a result of cluster and factor analysis carried out on the phytosociological data: three submerged (*Potamogeton pectinatus*, mixed submerged, and *Potamogeton pectinatus-Ceratophyllum demersum*); two floating leaved (*Nuphar variegatum* and *Potamogeton natans*); four emergent (*Equisetum fluviatale*, *Eleocharis palustris*, *Alisma plantago-aquatica*, and *Typha latifolia*); and three meadow (*Carex-Acorus calamus*, *Carex*-bryoid, and *Acorus calamus-Sonchus uliginosus*).

4. The successional sequence in these oxbows follows one basic pattern: *Potamogeton pectinatus*, *P. zosteriformis*, *P. richardsonii*, *Ceratophyllum demersum* → *Potamogeton pectinatus* → *Nuphar variegatum* or *Potamogeton natans* → *Equisetum fluviatale* or *Alisma plantago-aquatica* and *Eleocharis palustris* or *Typha latifolia* → *Carex* meadows → *Salix* shrub → *Populus balsamnifera*.

5. The maximum aboveground standing crop of communities follows a definite pattern with succession: from submerged (*ca.* 200 g/m^2), through floating leaved (*ca.* 210 g/m^2), to the emergent community (*ca.* 465 g/m^2) there is a stepwise

increase in annual production, which declines in the meadow community (*ca.* 325 g/m^2).

6. LAI does not change during the early stages of succession: all four community types studied had LAI's of 3 to 4.

7. Total chlorophyll per unit area follows a pattern very similar to standing crop, except that submerged communities (240-916 mg/m^2) contain more chlorophyll than floating leaved (293-797 mg/m^2). Emergents contain the most chlorophyll (622-2,127 mg/m^2), while meadow communities show a drop (542-1,414 mg/m^2) when compared with emergents.

8. Water chemistry and water level fluctuations, due to repeated flooding, appear to be the major factors controlling plant establishment, distribution, and succession. Water level fluctuation is the most important single factor, and controls the species composition of nearly all the early successional stages. Flooding also controls the rate of succession, since this is very much a function of sedimentation rates, by increasing the rate of sediment deposition. Flooding may also retard succession by the wholesale distruction of communities.

9. The difference in standing crop, and, by extension, productivity, of these successional stages appears to be the result of a combination of physical and physiognomic factors. Differences in light intensity, rates of carbon dioxide diffusion, and nutrient availability are responsible for the major differences between the productivity of aquatic (submerged and floating leaved) communities and semi-aquatic (emergent and meadow) communities. Productivity is also

affected by the height of the plant community and its structure. The taller a plant community, the greater the number of layers of photosynthetically active tissue, and the higher the probability of light being intercepted and utilized on a unit area basis. Structure and height of the communities examined correlate very well with their productivities, but LAI *per se* does not, indicating that structure is more important than the total photosynthetic area possessed by the plant community in determing its annual production.

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Appendix. Communalities of the Quartimax rotation presented in Table 8. The communalities are equal to the proportion of the variation of each community involved in the factor patterns.

Community	Oxbow #	Communality
Potamogeton pectinatus	2	0.943
Potamogeton pectinatus	4	0.990
Potamogeton pectinatus	6	0.985
Potamogeton pectinatus	7	0.990
Potamogeton pectinatus	8	0.990
Potamogeton pectinatus	11	0.995
mixed submerged	1	0.827
mixed submerged	3	0.916
mixed submerged	12	0.840
Potamogeton pectinatus-Ceratophyllum demersum	5	0.279
Nuphar variegatum	3	0.990
Nuphar variegatum	6	0.994
Nuphar variegatum	7	0.994
Nuphar variegatum	8	0.996
Nuphar variegatum	9	0.939
Potamogeton natans	4	0.991
Potamogeton natans	8	0.983
Potamogeton natans	12	0.990
Equisetum fluviatale	5	0.896
Equisetum fluviatale	8	0.948
Equisetum fluviatale	12	0.971
Eleocharis palustris-Beckmannia zyzigachne	2	0.806
Eleocharis palustris	8	0.937
Eleocharis palustris	15	0.951
Typha latifolia	10	0.560
Alisma plantago-aquatica	2	0.989
Alisma plantago-aquatica	15	0.986
Carex-Acorus calamus	9	0.898
Carex-Acorus calamus	10	0.748
Carex-Bryoid	5	0.560
Acorus calamus-Sonchus uliginosus	2	0.748

Appendix B. The length and surface area of the fifteen intensively studied oxbow lakes based on a map of the study area provided by the Division of Water Resources (scale 1" = 1 m.).

Oxbow #	Length (km)	Area (ha)
1	2.4	39
2	1.8	28
3	2.3	37
4	3.7	59
5	1.8	29
6	2.4	39
7	2.6	42
8	1.8	29
9	2.0	32
10	2.4	39
11	3.4	55
12	2.8	45
13	2.0	32
14	2.8	45
15	0.8	13

Appendix C. All species which appeared in the communities intensively studied with an average cover of less than 0.5% over the summer and all the species found along the banks in the Pembina River in the study area.

Species	Community and Oxbow[1]
	Submerged[2]
Chara sp.	PP6, PP11
Nuptans variegatum	MS3, PP8
Potamogethon natans	PP8
Potamogeton pectinatus	R
Potamogeton richardsonii	R
Sagittaria cuneata	PP11
	Floating Leaved[3]
Chara sp.	PN8
Cladophora sp.	PN8, PN12
Myriophyllum exalbescens	PN4, PN8, PN12
Najas flexilis	NV3, NV7
Potamogeton richardsonii	PN8
Sagittaria cuneata	PN8, NV9
Sparganium spp.	PN8, NV6
	Emergents[4]
Acorus calamus	TL10
Alisma plantago-aguatica	EF8, EP8, TL10
Alopecurus aequalis	APA2
Beckmannia syzigachne	EF5, EF8, EF12
Bidens cernua	EP2, EP15
Calamagrostis canadensis	EF8
Caltha natans	RB
Carex atherodes	EF8, EP8, EP2, TL10
Carex retrorsa	EP2
Carex rostrata	EP2, TL10, APA2
Carex stricta	RB
Carex sychnocephala	EF8, EP2
Ceratophyllum demersum	EF5, EF12, EP8
Cicuta bulbifera	EF8, TL10
Cicuta douglasii	EP2
Eleocharis acicularis	RB
Eleocharis engelmannii	RB
Eleocharis palustris	EF8, APA15, RB
Epilobium glandulosum	EF8, TL10
Erysimum cheiranthoides	APA15
Galium trifidum	EP2
Geum allepicum	EP8, EP2
Glyceria grandis	EF5, EF8, EP8, TL10
Hippuris vulgaris	TL10, RB

Appendix C. continued...

Species	Community and Oxbow
Hordeum jubatum	EF8, EP2
Juncus spp.	RB
Mentha arvensis	EF5, EF8, EP8, TL10
Myriophyllum exalbescens	EF8, EP8
Phalaris arundinaceae	EF5, EP2
Plantago major	EF8, EP2
Poa palustris	EP8, TL10
Polygonum (amphibium?)	EF8, EP8, EP2, APA15
Potamogeton natans	EP8
Potamogeton pectinatus	EP8, APA2
Potamogeton richardsonii	EP8
Ranunculus (sdl)	EF8, EP2, TL10
Ranunculus circinatus	EF5, TL10, RB
Ranunculus gmelinii	RB
Sagittaria cuneata	EF5, EF8, EF12, EP8, EP15, TL1
Salix spp.	EP2, TL10, RB
Scirpus microcarpus	RB
Scirpus validus	EF8, EP8, RB
Scutellaria galericulata	TL10
Sium suave	TL10, RB
Sonchus uliginosus	EF8, EP8, EP2
Sparganium spp.	EF5, EP8, EP2, TL10, APA15
Stachys palustris	EF8, EF12, EP2
Stellaria longipes	EF12, EP8, APA15
Taraxacum officinale	EF8, EP15
Utricularia	EF5, EP2, TL10
	Meadow[5]
Alisma plantago-aquatica	AS2
Arabis hisuta	CA10
Beckmannia syzigachne	AS2
Bidens cernua	CA10
Brachythecium salibrosum	CA9, CB5
Bryum sp.	CA9, CB5
Calamagrostis canadensis	CA10
Carex stipata	AS2
Carex stricta	AS2
Carex synocephala	AS2
Cicuta bulbifera	CA9
Cicuta douglassii	AS2
Cirsium spp.	CB5, AS2
Epilobium glandulosum	CA10, AS2
Equisetum fluviatale	CA9, CA10, CB5, AS2
Geum allepicum	CB5
Glyceria grandis	AS2
Leptodictyum trichopodium	CA9, CB5
Marchantia polymorpha	CA10, CB5
Mentha awensis	CA9
Mnium cuspidatum	CB5
Petasites saggitatus	CA9, CB5
Pholia mutans	CA9, CB5
Polygonum coccineum	CA9, CB5, AS2
Potentilla anserina	CB5

Appendix C. continued...

Species	Community and Oxbow
Ranunculus (sdl)	CA9, CA10, AS2
Rumex sp.	AS2
Salix spp.	AS2
Scutellaria galericulata	CB5
Sium suave	CA10, CB5, AS2
Sonchus uliginosus	CB5
Stachys palustris	AS2
Stellaria longipes	CA9, CA10, CB5
Tanecetum vulgare	CB5
Typha latifolia	CA9

1 Community and oxbow are represented by an abbreviation of the community name followed by the number of the oxbow in which it is found.

2 PP - *Potamogeton pectinatus*
M - mixed submerged
R - river

3 PN - *Potamogeton natans*
NU - *Nuphar variegatum*

4 EF - *Equisetum fluviatale*
EP - *Eleocharis palustris*
APA - *Alisma plantago - aquatica*
TL - *Typha latifolia*
RB - river bank

5 Ca - *Carex* - *Acorus calamus*
CB - *Carex* - Bryoid
AS - *Acorus calamus* - *Sonchus uliginosus*

Appendix D. Species found in the *Salix* shrub, *Salix* forest and *Populus balsamifera* forest.

Species	Community[1]
Achillea sibirica	SS, SF
Agropyron repens	SF, PB
Anemone canadensis	PB
Aster sp.	SS
Aster ciliolatus	SS, SF
Aster foliaceus	SF
Betula pumila	SS
Calamagrostis canadensis	SF, PB
Calamagrostis inexpansa	SS
Caltha palustris	SS, SF
Carex rostrata	SS
Carex simulata(?)	SS
Carex stipata	SF
Cirsium arvense	SS, PB
Cornus canadensis	SF
Cornus stolonifera	SS, SF, PB
Crepis tectarum	SS
Epilobium glandulosum	SS
Eguisetum fluviatale	SS
Eguisetum pratense	SF, PB
Geum allepicum	SS
Galium boreale	SS, SF
Galium trifidum	SS
Galium triflorum	SF, PB
Glyceria grandis	SS
Lathyrus ochraleucus	SS, PB
Marchantia polymorpha	SS
Maianthemum canadense	SS, SF, PB
Mentha arvensis	SS
Menyanthes trifoliata	SS
Mitella nuda	SF
Parnassia palustrus	SS
Petasites sagittatus	SS
Poa palustris	SS, SF
Populus balsamifera (sdl)	SF
Populus balsamifera	PB
Populus tremuloides (sdl)	SF
Potentilla anserina	PB
Ranunculus spp.	SF, PB
Ribes oxyacanthoides	SS, SF, PB
Rosa acicularis	SF, PB
Rumex sp.	SS
Salix spp.	SS, SF, PB
Scutellaria galericulata	SS, SF
Senecio spp.	SF, PB
Smilacina stellata	SF, PB
Sonchus arvensis	SS, PB
Stellaria longipes	SS

Appendix D. continued...

Species	Community
Taraxacum officinale	SF
Urtica major	SS, SF
Viburnum trilobum	SS, SF, PB
Vicia americana	PB

[1] SS - *Salix* shrub
SF - *Salix* forest
PB - *Populus balsamifera*

Appendix E. Formula used to calculate the percentage of the variation accounted for by an ordination when compared with the calculated dissimilarities between community pairs

$$X = \frac{\Sigma \, dij}{\Sigma \, Dij} \times 100$$

where X = percent of the variation accounted for by the ordination;

dij = the distance between any two communities i and j on the ordination diagram in the same units as the calculated dissimilarities;

Dij = the calculated dissimilarities between communities i and j.

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